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of the

Torrey Botanical Club

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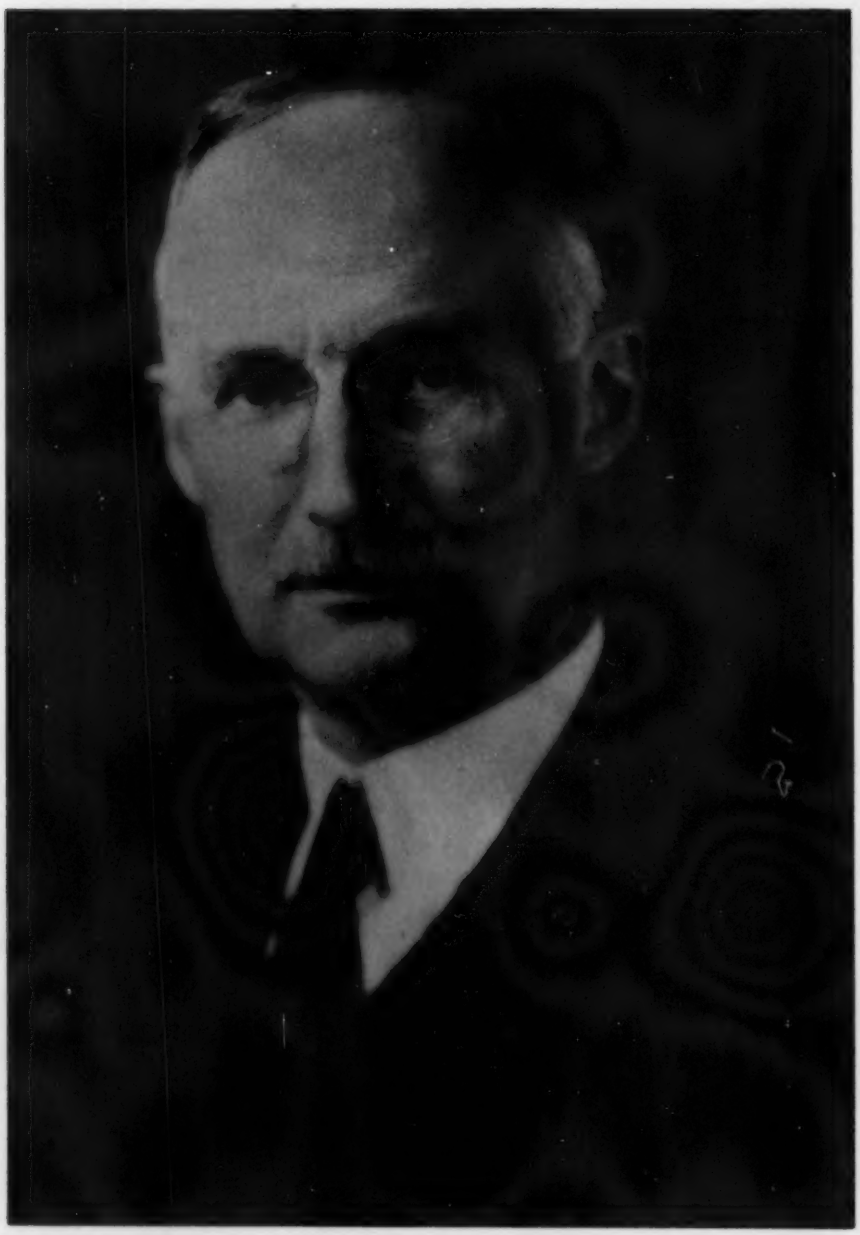

TRACY ELLIOT HAZEN

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, NO. 6, PP. 559–562 NOVEMBER, 1943

TRACY ELLIOT HAZEN

1874–1943

CORNELIA L. CAREY, HAROLD C. BOLD AND JOHN HENDLEY BARNHART

Professor Tracy Elliot Hazen, distinguished botanist and honorary life member of the Torrey Botanical Club, died March 15, 1943, at Waterbury, Connecticut, after several years of declining health. He was the youngest of seven brothers, three of whom, Rev. Carleton Hazen of Middletown, Connecticut, Rev. William Hazen of Auburndale, Massachusetts and Dr. Robert Hazen of Thomaston, Connecticut, survive him. He was born July 4, 1874, in Jericho Center, Vermont, the son of Rev. Austin Hazen and Mary Jane (Carleton). His early years were spent in the vicinity of his birthplace, where he had ample opportunity to develop his life-long interest in plants.

He prepared for college at the Mount Hermon School, and was graduated from the University of Vermont in 1897 with the A.B. degree, Magna Cum Laude. He was elected to membership in Phi Beta Kappa at this time. As a student he was keenly interested in the study of the classics, and his decision to devote his major interest to botany was the occasion of disappointment for faculty members of the classical department. In this connection he often recalled the stimulation and encouragement he had received from Professor L. R. Jones, at that time in charge of the botanical work at Vermont. The meticulous care and critically keen powers of observation, which are so characteristic of Dr. Hazen's later publications and researches, are already apparent in his senior thesis on *Sphaerella lacustris*, a study which he later elaborated and published as a Memoir of the Torrey Club. The beautifully colored illustrations from this paper have been reproduced in numerous texts. Dr. Hazen remained a loyal son of the University of Vermont, returning frequently to participate in the alumni activities during the annual Commencement week.

During the three years, 1897–1900, he pursued graduate studies in botany and zoology at Columbia University, receiving the A.M. degree in 1899 and the Ph.D. the following year. At the suggestion of Professor L. M. Underwood, he carried on critical taxonomic studies of the filamentous Chlorophyceae. The results of these studies were ultimately published in the eleventh volume of the Memoirs of the Torrey Club. He became an indefatigable collector during this work. During this period he was elected to membership in the Torrey Botanical Club, in the activities of which he maintained an active interest until his death, serving as its president in

The portrait of Doctor Hazen is published with the assistance of the Lucien M. Underwood Memorial Fund.

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1934 and 1935, as associate editor in 1903–1911 and 1932–1939, and as editor in 1924–1931. After forty years of loyal service and annual membership he was elected an Honorary Life Member in 1939.

Dr. Hazen served as Director of the Fairbanks Museum of Natural Science at St. Johnsbury, Vermont, during 1901–1902, continuing his collection and study of the algae, as well as of the ferns and flowering plants. He returned to Columbia as assistant in the Department of Botany from 1902 to 1903. In January of the latter year he was called to Barnard College as Tutor, to continue the work of Miss Lonise B. Dunn, who had died. Thus began an association with that school which was to continue for thirty-six years. He attained to the rank of associate professor which he held at the time of his retirement in 1939.

The years at Barnard were exceedingly fruitful in research (much of which remains unpublished), and more especially in teaching. Few others have given so unstintingly, so unselfishly, and with such complete devotion to their students. Professor Hazen was driven by his ideal of providing living specimens in various stages of development for his students; he spared no effort, time or expense in realizing it. In the early years he traveled long distances by bicycle through New York City and its suburbs collecting the necessary material. Later, the excursions were made by public conveyance, always at his own expense. His hundreds of carefully chosen microscopic preparations were personally prepared and greatly enhanced the value of his courses for the student. He had an uncanny ability for transmitting his own extremely keen powers of perception to his students, and was never content until the dullest of the group had correctly observed and understood the most obscure features of the specimen before him. He was unflinchingly zealous in accomplishing this purpose, giving ungrudgingly of his leisure hours to all who sought help. Teaching of this high order is unfortunately all too rare.

His research interests were fundamentally in the Chlorophyceae, more especially the unicellular Volvocales; wherever he traveled he studied, preserved, and prepared notes and illustrations of the local representatives of the group. Many plates of beautifully colored illustrations executed during these studies bring to light a number of species and several genera new to science; it is hoped that these may be published. He was abundantly endowed with the patience, keenness and perseverance necessary for the critical study of these motile organisms. His publications on *Lobomonas* and *Brachiomonas* reflect countless hours of grueling, long-continued microscopic observation, which were rewarded by a completeness of understanding of their structure and reproduction, scarcely equaled by others. His failure to publish much of his work may be attributed to his inordinately high ideals of perfection and thoroughness. In addition to the algae, Professor Hazen

maintained a lively interest in the angiosperms, and in this connection published his well known study of trimorphism in *Pontederia*.

Professor Hazen traveled quite extensively in Europe, South America, and the West Indies, collecting and studying the local floras, and at the same time nurturing his increasing interest in genealogy. He was a member of a botanical expedition to the high Andes of Colombia in 1922, and of Dr. Britton's expeditions to Trinidad in 1920 and to Porto Rico in 1924.

In addition to his duties at Columbia, Professor Hazen taught in the course on algae at the Marine Biological Laboratory, Woods Hole, Massachusetts, during the summers of 1924 and 1926, and served in a similar capacity at the Hopkins Marine Station, Pacific Grove, California, during the summer of 1930.

For a number of years he served as an appointed member of the Board of Managers of the New York Botanical Garden from the Torrey Botanical Club, and was also a member of the Corporation of the Botanical Garden until 1942. He represented the Torrey Botanical Club at the International Botanical Congress in Amsterdam in 1934, at the Centenary Celebration of the Botanical Society of Edinburgh in 1936, and at the meeting of the British Association for the Advancement of Science in 1938. In spite of extreme debility, and against his physician's advice, he attended the celebration of the seventy-fifth anniversary of the Torrey Club in June 1942. This proved to be his last opportunity for active participation in the Club's activities.

After retiring Professor Hazen gave himself more fully to genealogy, and achieved considerable distinction and recognition in this field. He wrote several papers of genealogical interest which were published in the New England Historical and Genealogical Register in 1939 and 1940 as *Contributions for the Tercentenary of Rowley, Massachusetts,* and left a number of other papers in manuscript. In recognition of his scholarship he was invited in 1939 to deliver the main address at the celebration of the Tercentenary of Rowley, Massachusetts.

Beside the Torrey Botanical Club Professor Hazen held memberships in a number of other societies, among them the American Association for the Advancement of Science, the Botanical Society of America, the Marine Biological Laboratory, the New England Botanical Club, the Connecticut Botanical Society, the American Fern Society and Sigma Xi. He was also a member of the Vermont Historical Society, the Massachusetts Historical Society, the New England Historic Genealogical Society, the Society of Colonial Wars in Massachusetts, the Society of Mayflower Descendants in Connecticut and the Society of Sons of the American Revolution.

In a letter to Professor Hazen's family the Corresponding Secretary of the Club has aptly summarized the sentiments of its members in writing:

" . . . the Torrey Botanical Club was singularly fortunate in having profited by the sound scholarship, the meticulous labors, the faithful devotion to duty, and the kindness of heart of Professor Tracy E. Hazen. All its members admired him, all respected him as a thorough gentleman, and all who knew him intimately loved him."

The published work of Tracy Elliot Hazen

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The seventh annual winter meeting of the Vermont Botanical Club. Rhodora **4**: 64. 6 Mr 1902.

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Proceedings of the Club: March 8, 1904. Torreya **4**: 73, 74. 13 My 1904.

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Proceedings of the Club: October 13, 1908. Torreya **8**: 265, 266. 25 N 1908.

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The trimorphism and insect visitors of *Pontederia*. Mem. Torrey Club **17**: 459–484. *pl. 14, 15; f. 1–12*. 10 Je 1918.

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The phylogeny of the genus *Brachiomonas*. Bull. Torrey Club **49**: 75–92. *pl. 3, 4; f. 46–50*. 18 My 1922.

New British and American species of *Lobomonas:* a study in morphogenesis of motile algae. Bull. Torrey Club **49**: 123–140. *pl. 5, 6*. 15 Je 1922.

Flora of Penikese, fifty years after: Algae of fresh water. Rhodora **26**: 211, 212. 5 Ja 1925.

Flora of Penikese, fifty years after: Algae of brackish water. Rhodora **26**: 215. 5 Ja 1925.

Botanizing in the Colombian Andes. Jour. N. Y. Bot. Gard. **26**: 132, 133. (30) Je 1925.

The English ancestry of Edward Carlton of Rowley, Mass. New Engl. Hist. Geneal. Reg. **93**: 3–46. *pl.; chart.* (1) Ja 1939.

The ancestry of Ellen Newton, wife of Edward Carlton of Rowley, Mass. New Engl. Hist. Geneal. Reg. **94**: 3–18. *pl.; f.* (1) Ja 1940.

(With Harold Charles Bold) New motile algae from New Jersey. (Abstract.) Am. Jour. Bot. **26**: Suppl. 25. 4 Ja 1940.

Two founders of Rowley, Mass. New Engl. Hist. Geneal. Reg. **94**: 99–112. *pl.* (1) Ap 1940.

Contributions for the tercentenary of Rowley, Massachusetts. (Ap 1940) This comprises separates of the three genealogical papers of 1939 and 1940, with a general title-page.

BARNARD COLLEGE, COLUMBIA UNIVERSITY, AND
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BULLETIN OF THE TORREY BOTANICAL CLUB

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THE OSMOTIC QUANTITIES OF THE CELLS IN THE HYPOCOTYL OF HELIANTHUS ANNUUS SEEDLINGS[1]

WILLIAM A. BECK AND BASILIA ANDRUS

INTRODUCTION

In recent years great interest has been manifested in the nature of growth in plants by cell enlargement. In particular a source of energy has been sought which would satisfactorily account for the phenomenon of the enlargement of the plant cell. The older notion that turgor is entirely responsible for the enlargement became untenable with the discovery of Ursprung and Blum that the turgor in the growing root cells of *Vicia faba* is minimum in the zone of maximum growth. More recently an active growth of the cell wall was made accountable for the phenomenon. The auxin was made responsible for this growth of the wall, but for some time it was not clear if the auxin caused it directly or only by acting inductively upon the protoplast. Growth of the wall by intussusception can hardly be doubted in view of recently proved facts, and there can be little, if any, doubt that this growth of the wall is due to the addition of materials elaborated by the protoplasm, which is influenced in its activity by the growth-promoting substance. It is probable that the influence of auxin evokes, not only the elaboration of the necessary wall material, but other growth phenomena as well, such as the production of the solutes necessary to maintain the turgor of the growing cells.

It is the purpose of the present study to investigate carefully the active growth of developing cells and their osmotic quantities, with the end in view of correlating these phenomena and drawing such conclusions as are possible regarding changes in the physical nature of the protoplast, the cell sap, and the wall. The results should give a better understanding of the nature of growth by cell enlargement, and of the energies which are involved.

The terms expressing osmotic quantities have been used in such a variety of meanings that one is in doubt many times about their real significance when used by an author who fails to define his terms accurately. For that reason care is taken here to define each term and state its significance. For a review of the literature on this subject the reader is referred to the works of Ursprung (44, 46), Beck (3), and Stark (40).

In plant physiology the term osmotic quantity is employed to designate any of the quantities which refer to such pressures or tensions in the living

[1] The cost of publication of this paper was assisted by the Institutum Divi Thomae, Bradley Hall, Palm Beach, Florida.

plant cell as depend directly or indirectly upon osmotic phenomena, including components that result from combinations of these elementary vector quantities.

In previous work on growth phenomena and pigment production (6, 7, 9, 10, 12, 13, 14, 15), *Helianthus annuus* was used; it was natural to choose the same object for experimental study in the present work since a body of data regarding these seedlings is on hand. From previous experience and careful propagation each year it was possible to have strictly comparable plants from seeds of the same strain grown under identical conditions.

Ruge (35, 36) studied the hypocotyl of *Helianthus* seedlings in an effort to determine the influence of heteroauxin on cell enlargement, and recorded osmotic quantities determined by him which may well be compared with the data we present here. But it must be remembered that the regions of the hypocotyls which he employed are not the same as in our experiments and he cultured his seedlings somewhat differently. His seedlings were not of the same age or size as ours and he confined his studies to the cortical tissue, while we studied both the epidermal and cortical tissues. The exact determination of the osmotic quantities is tedious and involved; it demands much time, so that conceivably Ruge was obliged to give less attention to this phase of his work, considering the many and varied operations that he was obliged to carry out within a limited time to achieve his objective. He followed Ursprung's methods for the determination of some of his quantities, but it is not clear if he did so for all.

We proposed to give close attention to the exact determination of the osmotic quantities in normally developing cells, that is, from the time the cells cease to proliferate to the mature state. Our work extended over a period of three years.

METHODS

Etiolated *Helianthus* seedlings, 90 hrs. old, grown under controlled conditions (90 per cent relative humidity and 25° C) were employed. At this age the plants were approximately 45 mm. high. From previous work it was concluded that the cells of the hypocotyl proliferate directly below the base of the cotyledons within a distance less than 2 mm. from the base of the cotyledons, and at a distance of 35 mm. the cells were certainly mature. Accordingly the hypocotyl was divided into seven zones, each 5 mm. long as indicated in figure 1, and the osmotic quantities were determined for the cells of each zone.

The methods devised and described by Ursprung (45) were followed in this work. Our results do not refer to individual cells but to sections of specific tissues. Sucrose was used as a plasmolyzing agent, since it is better than any other agent (2, 20, 41, 51). It is well to remember when comparing our

results with those obtained by Ruge (35) that he used dextrose as his agent in some of his studies.

For the determination of cellular dimensions the eyepiece micrometer of

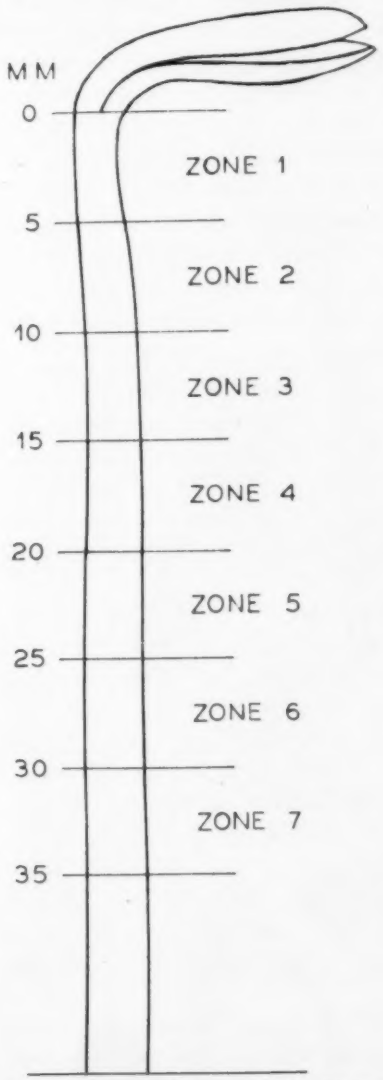

FIG. 1. *Helianthus* seedling as used in the experiments.

the regular microscope was employed, but for the dimensions of sections of tissues and variations of their lengths a special measuring microscope was employed in which the error was not more than $\pm$ 0.01 mm.

The order in which the various osmotic quantities were determined was not the same as that followed in the presentation of the work. In the laboratory the order was as follows: first the determination of the sizes of the cells in the normal state, while immersed in paraffin oil; and then the suction tension of the cells by direct measurement; the osmotic value at incipient plasmolysis; and the osmotic value at saturation; together with the respective sizes of the cells in the three states; finally the wall pressure was determined.

For the sake of clarity the data will be presented in the following order: the cellular dimensions and cellular characteristics will be discussed first; and will be followed by the osmotic value of the cell sap in the three states; and the suction tension of the cell as an entity; finally the wall pressure will be discussed.

CELLULAR DIMENSIONS AND CHARACTERISTICS

Discussion of the Cells and Their Walls. Before discussing the osmotic quantities of the cells at different ages it is well to have a clear understanding of the general appearance of the plants which were employed and the sizes and characteristics of the cells at different stages of development.

In figure 1 a diagram of a typical seedling is given. This may well be taken as a diagram of the average form and size of all that were used. Care was taken to draw it exactly to size from a specimen that was considered the average.

The smaller diameter of zone 1 is characteristic. Under the conditions of culture the seedlings were etiolated and the carotene and xanthophyll were chiefly located in the cotyledons and the uppermost region of the hypocotyl. The rest of the hypocotyl is opaloid. No effort was made to determine whether the pigment deteriorated with the enlargement of the cells or whether it was merely masked by the total reflection of light in the intercellular spaces formed in the cortical tissue as the hydrostatic pressure of the cells increased in that tissue. Since it has been suggested that the carotinoid pigments may be a part of the respiratory mechanism it is desirable to investigate the possible correlation of pigment production and cell enlargement. If these pigments affect the auxin activity in the protoplast, cell enlargement may in turn be influenced by the presence or absence of these pigments (8, 9).

It was not considered necessary to study regions which lay further removed from the cotyledons than 35 mm. because beyond 25 mm. the cells may be considered mature, as was shown by Beck and Donnelly (13).

It is important in such studies as we have in hand to recognize the distribution of the growth zones, hence a very careful study of the dimensions of the cells in each of the seven zones was made and the results are recorded in table 1.

The length of the cells was determined with the aid of the eyepiece micrometer. The determinations were made at three points in each zone, the uppermost, the lowermost, and the midregions, and the average of these was recorded in table 1. It was considered sufficient to determine the length of the cells as an expression of their enlargement, since actual measurement proved that the diameter of the cells was almost the same in all seven zones. This is in agreement with the fundamental rule that was first suggested by Czaja (19) and verified by Ruge (35) for the hypocotyl of *Helianthus* seedlings, and was further confirmed by Borgström (17), that the cell walls grow in a polar manner increasing their mass in the lateral walls but not appreciably in the transverse. Since the development of the stomatal complexes distorts the neighboring cells, these regions were avoided. No particular difficulty was experienced in the study of the cortical cells.

The cells directly beneath the cotyledons were compressed in general appearance. This region did not extend much beyond 1 mm. and certainly not beyond 2 mm. This is evidently the zone of cell proliferation, and the region in which auxin is produced. The auxin which is present in the remaining 3 mm. of zone 1, in which the cells have begun to enlarge, is probably the auxin which was formed in the uppermost 2 mm. and is in the process of translocation (12).

Since the cells of zone 1 are possessed of a relatively small cell sap cavity, when it is not entirely lacking, reliable figures regarding osmotic quantities can hardly be expected. Our results are, however, included in the table for the sake of completeness. In an effort to interpret the results it must be borne in mind that the forces refer predominantly to the phenomenon of imbibition in this zone. Plasmolytic methods when applied in very young cells yield more or less doubtful results for another reason; namely, that the undeveloped cell walls lack elasticity and rigidity, so that when they are expanded beyond the limits of elasticity in any operation, they do not readily recede with the protoplast when an attempt is made to plasmolyze the cell. It was for this reason that Overbeck (30) and Oppenheimer (29) criticized Ursprung's method of determining the suction tension. To avoid any similar error we modified Ursprung's strip method. After first determining the suction tension by Ursprung's original method in order to obtain threshold values, we made as many independent sections as we deemed necessary, and immersed them simultaneously in graded solutions above and below the threshold values. Each strip was immersed only once in a solution of specific concentration. The size of each strip was determined before immersion and again after immersion. The solution in which a strip failed to alter its size was evidently in equilibruim with the cells. In this manner the possibility of stretching the walls beyond the limits of elasticity was avoided.

In view of the fact that there is some discussion regarding the manner in which the volume of the cell enlarges, i.e., whether it enlarges by the insertion

of new material or whether only passively by a process of stretching it beyond the limits of elasticity under the stress of the hydrostatic pressure from within, it was thought well to measure the thickness of the cell wall in the different zones. Unfortunately we were not equipped to do this with sufficient exactness, since our instrument error using the eyepiece micrometer was too great. We did, however, make an attempt to get what information we could by this method.

Frey-Wyssling (22), employing the double refraction method, proved that the cellulose chains of the cell walls of grasses shift during certain phases of growth. Ruge (36), employing the same method, concluded from his experiments that such shifting of the chains occurs in *Helianthus* seedlings in a zone about 4 to 5 mm. long directly beneath the cotyledons. Accordingly he holds that in this zone the cell wall is stretched beyond the limits of elasticity by the inner hydrostatic pressure. Our own less exact methods lead to the same conclusions. This conclusion is probably true in the lowermost region of the first zone. The fact that the diameter is less in the first zone than in the rest of the hypocotyl is in agreement with this conclusion. It was evident to us that the walls of the epidermis became thinner as growth proceeded in the first zone. In the older zones the cell wall became thicker progressively. In the cortical tissue it was more difficult to come to a decision, but there were no contradictory data to prevent us from agreeing with Ruge, that in the very young cells not much material is added to the cell wall by the process of intussusception, but at a distance of more than 6 mm. from the base of the cotyledons there is evident growth of the wall by intussusception (36).

The participation of turgor in the process of growth by cell enlargement has long been a subject of discussion. In 1924 Ursprung and Blum (47) pointed out that turgor is least in the region of greatest growth. In our studies we have found that turgor, or its equilibrant the wall pressure, is least in this region, but not least at the point of inflection of the growth curve, that is at a distance of 6.5 mm. from the base of the cotyledons (10, 14). In our studies of wall pressure we have found that the value is least at a distance of 20 mm. from the base of the cotyledons in the epidermis and at a distance of 15 mm. in the cortical tissue (see figure 5).

Contraction and Expansion of the Cells. The contraction of normal cells when plasmolyzed is very interesting. It was determined by direct measurement and the results are recorded in table 1. When the size of the cell at incipient plasmolysis was plotted against the distance from the base of the cotyledons the curves for both tissues were found to be typical growth curves just as was found to be true for the cells in the normal state (10, 14). This is clear evidence that the walls grow actively, since the walls were not thinner in older than in younger cells, and therefore there could not have

been more stretching beyond the limits of elasticity. The per cent contraction is not the same for the two tissues and does not vary from the average so much in the epidermis as it does in the cortical tissue, an evident indication that the nature of the wall is not the same in the two tissues. The epidermis shows least ability to contract in the second zone and greatest ability in the third, fourth, and fifth, and then definitely declines in the sixth and seventh zones (see table 1 and figure 2). The cortical tissue also manifests a low

TABLE 1. *Sizes of Cells in the Normal, Plasmolyzed, and Saturated States.*

Zone	Incipient Plasmolysis				Normal State		Water Saturated			
	Epidermis		Cortical		Epidermis	Cortical	Epidermis		Cortical	
	Length in Microns	Contract. in Percent	Length in Microns	Contract. in Percent	Length in Microns	Length in Microns	Length in Microns	Expansion in Percent	Length in Microns	Expansion in Percent
1	26.1	1.88	47.31	1.639	26.6	48.1	27.8	4.511	53.816	12.095
2	96.0	1.031	79.38	2.601	97.0	81.51	99.0	2.165	90.198	10.660
3	138.6	2.395	108.14	3.360	142.0	111.90	143.3	0.915	125.517	12.169
4	169.8	1.850	142.36	1.950	173.0	145.2	178.8	3.352	161.298	11.087
5	194.0	2.513	165.06	1.040	199.0	166.8	204.0	2.513	180.624	8.289
6	209.0	1.786	185.34	1.260	212.8	187.7	215.0	1.034	192.563	2.591
7	218.4	1.533	207.58	0.683	221.8	208.9	224.3	1.127	216.407	3.594

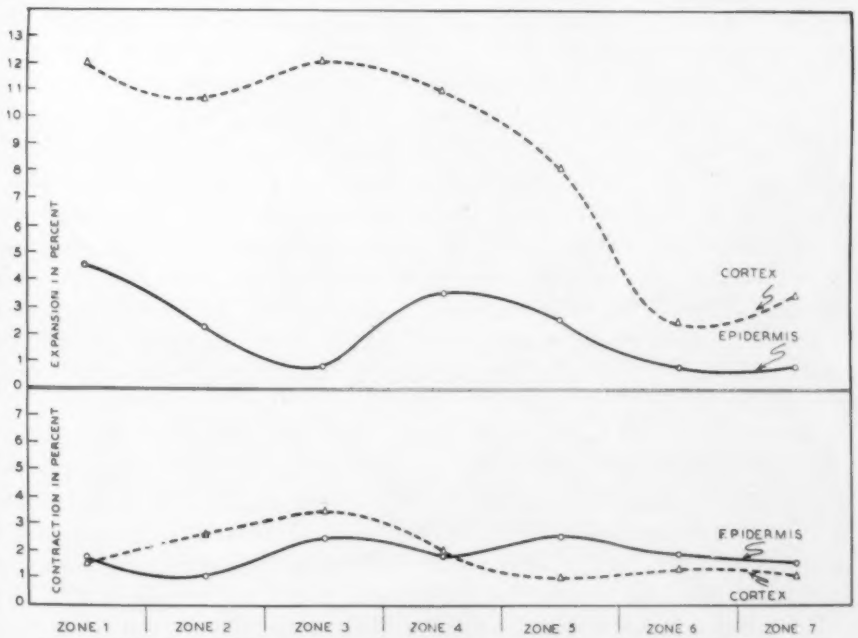

FIG. 2. Variation of the sizes of the cells from the normal, expressed in per cent, at plasmolysis and saturation for the seven zones.

ability to contract in the first zone, but then rises to a maximum in the third, after which there is a steady decline in the older zones where it is lower even than in the epidermis. From this it may be concluded that in the older zones either the cells in their normal state lack water (O_n and O_g being nearly equal might indicate but not prove as much; see table 2) or the walls cannot contract much in the two tissues because of the lack of elasticity. Since the suction tension is relatively low in the older zones there can hardly be a lack of water, so that the low ability to contract must be ascribed to the nature of the wall, i.e. in zones six and seven the epidermis becomes rather rigid, and the cortex becomes more rigid as early as in the fourth zone.

The expansion of normal cells when placed in water was also determined by direct measurement. The cortical tissue shows considerably greater ability to expand than does the epidermis, particularly in the uppermost five zones. This is not difficult to understand from the respective structure and functions of the two tissues.

The ability to expand decreases temporarily in the first three zones and rises to a secondary high in the fourth, and thereafter decreases steadily. In the cortical tissue the ability to expand is unusually high in the first zone and sinks temporarily in the second zone to rise in the third zone to a secondary high, after which it decreases rapidly to the *all* low in the mature cells, almost equal to the low of the epidermal cells. It is interesting that the ability of the epidermis to expand is low in the third zone when it is high in the cortical tissue, which indicates that the development of the cell walls is not identical in the two tissues.

The ability to contract is a safer indication that the wall is elastic than is the ability to expand: if the wall will neither contract nor expand readily it is evident that the walls are rigid. If the walls expand readily, but do not contract readily the indication is that the walls are plastic and that the water supply has not been sufficient to allow further expansion (otherwise they should be stretched beyond the limits of elasticity), either because the water had to be raised in the plant against the force of gravity, or because the potential difference between neighboring suction tensions was not sufficient to allow water to flow readily into the cells. If there is a fair degree of expansion and contraction as well, the indication is that the wall is neither plastic nor rigid, i.e. moderately elastic.

Interpreted in this sense our data show that the epidermis is very plastic in the first two zones, less so in the succeeding ones. In the third zone the contraction is high and the expansion low, accordingly the elasticity is high. The elasticity is maximum in the fourth zone where both contraction and expansion are high. In the more mature epidermal cells both expansion and contraction decrease; that is, the walls are evidently more rigid.

The cortical tissue develops somewhat differently. The degree of contraction is low in the first zone where the extensibility is high, indicating great

plasticity. In the third zone both the expansion and the contraction are high, i.e. maximum elasticity exists. From this point on the expansion as well as the contraction decrease steadily, clearly indicating that the walls are becoming rigid.

From the respective values for the two tissues it is evident that the cortical cells have far less rigid walls than do the epidermal cells, which is as might be expected from a consideration of the respective functions of the two tissues.

It is particularly interesting to study the diagram in figure 1. In agreement with the macroscopic determination of the diameter of the hypocotyl in the first zone, the cells in this zone are always somewhat less in diameter than the cells of the older zones. Only well along in the second zone is the nearly constant diameter attained. If it is assumed that the walls are plastic and that the osmotic turgor develops slowly and the suction tension, nevertheless, remains high, it is evident that the high suction tension is due to the imbibition of the protoplast and is essentially non-osmotic in nature.

Characteristics of the Protoplast. (a) *Gradients.* There is a characteristic gradient of viscosity in the protoplasm of the cell of the hypocotyl of the seedlings, ranging from the zone of cell proliferation to the enlarged, mature cell. We verified this by direct experiment but are not listing our results because they do not show anything more than is already recorded in the literature by Strugger (41) and Ruge (35). There can be no doubt of this fact in the particular case of *Helianthus* seedlings. It appears to be a general fact that young protoplasm is more viscous than older protoplasm, since it was proved in algae and fungi as well as in various organs of the higher plants (18, 26, 34, 49, 50).

It is generally admitted that protoplasm is a complexly built mixture of hydrophilic colloids and we are accordingly justified in applying to it the principles of colloid chemistry. Physico-chemical experiments have shown beyond reasonable doubts that the relative viscosity of a substance is a good indicator of its relative colloidal state. A knowledge of the changes in viscosity of the protoplasm, such as are indicated by the gradient manifested in the developing cells of the sunflower seedlings, aids in a better understanding of changes that occur in the colloidal state of the protoplasm.

The viscosity has been brought into correlation with growth and growth-promoting substances by Strugger (42) employing the hypocotyl of *Helianthus* seedlings, who found that the young cells of the stretching zones require a greater length of time for the protoplast to become rounded off in a plasmolyzing solution than do mature cells, and he concludes that they consequently possess a higher internal non-osmotic pressure expressing itself by a greater viscosity. Ruge (35) obtained similar results. We repeated these experiments and obtained similar results. From the facts recorded in the

literature it is evident that we can express ourselves regarding the characteristics of the protoplasm in the seven zones of our seedlings such as its swelling ability, its stability, and its electrical charge. The swelling power of the protoplasm is considerable in the first zone and negligible in the others; there is a definite gradient from the younger cells to the older ones which is termed the plasmolytic gradient. This must, of course, be borne in mind when interpreting our results, since no effort was made to distinguish between the suction tension which is produced by the suction tension of the cell sap (due to osmosis) and that produced by the suction tension of the protoplasm (due to imbibition). Bennet-Clark, Greenwood, and Barker (16) considered it possible that active "secretion" of water takes place from the protoplast into the cell sap cavity, but it would hardly be justified to consider the increment of water in the cell sap cavity as a kind of synaeresis, since there is active production of solutes as the cells grow older (10, 14). No doubt, the cell sap concentration must bear some relation to the viscosity and the colloidal state of the protoplast, so that the protoplasm is constantly in dynamic equilibrium with its aqueous environment.

Pfeiffer (31, 32, 33) proved that a definite degree of viscosity in the cytoplasm is correlated with a definite electrical charge of the plasma colloid. When the electrical charge is changed then also an electro-viscosity effect must follow. The growing and non-growing cells are accordingly characterized by this, that the variations of the plasma ampholytes from the isoelectric point (I.E.P.) are different. The mature cells are "fixed."[2] There is sufficient experimental evidence in the literature regarding the cH gradients in relation to the differentiation of tissues to warrant the employment of the "plasmatic gradients" as visible expressions of the cH gradients which proceed in the same direction (24, 25, 37, 38).

The established cH gradient is significant for another reason, namely that it suggests a correlation of growth by cell proliferation and cell enlargement. It is well established that there is a difference of electrical potential between the chromatin of the nucleus and the cytoplasm; the nucleus being electro-negative and the cytoplasm electro-positive. Since cell proliferation, which is known to be rhythmic, ceases in the hypocotyl a short distance from the base of the cotyledons, and cell enlargement occurs in a graded manner parallel with the viscosity and the cH gradient, and is also rhythmic, the whole process of cell enlargement, which is known to be induced by natural auxins and heteroauxins (which are characteristically acid in reaction) must be related. It is extremely difficult to consider the function of the chromatin

[2] Because of the ampholyte nature of the protoplast a critical point must be reached at a very definite hydrogen ion concentration, in which the number of anions and cations is the same in their minimum. At the isoelectric point their cH is zero, in which therefore the electrical charge of the colloid is zero, and the number of neutral particles is maximum (cH = O at I.E.P.).

from a purely material concept basis without involving orientating forces, directed outward from bio-molecular electro-magnetic fields.

(b) *Discussion of the Characteristics.* There can be no doubt about the generation of auxin in the zone of cell proliferation. The manner in which it acts to cause cell enlargement and its translocation are not very clear. How gravity influences the auxin is particularly obscure; if it occurs in the form of pure solution gravity cannot affect it, and if it is not in pure solution its translocation by diffusion becomes impossible. These facts suggest that the auxin exercises its influence in a manner comparable to that of "evocators" (27).

Auxin must definitely be regarded as a phytohormone and consequently specificity, such as is attributed to bio-regulators in general, must characterize it. One of the outstanding marks of protoplasm is its specific ability to synthesize asymmetric compounds in which the atoms of the molecules are arranged in a specific asymmetry that cannot be duplicated in inorganic systems. Asymmetry points to a labile, dynamic, spatial arrangement of the atoms in the molecule, and the aging of cells may be regarded as a trend towards stable equilibrium within the bio-molecules. The more unstable the molecule, the greater the free energy content. The forces exercised by highly labile asymmetric molecules of the young proliferating cells directly beneath the cotyledons, through their asymmetry-inducing energy upon other molecules, may be assumed to play a very important role in influencing the growth of the older cells by cell enlargement, the material expression of this would be the formation of auxin.

Science has traveled far since Van't Hoff and LeBel laid the foundations for the science of stereo-chemistry. The valence in a material is no longer considered in a mechanical manner, but is linked to its configuration of electrons and its system of waves. The phenomena attending the asymmetric organic molecule are far more readily interpreted by means of the energy concepts of modern atomic theories than by means of the older theories of the classical physicists. The cH gradient suggests that the "trigger energy" which directs the process of cell enlargement, resides in the chromatin and that it is maximum in the young cells and minimum in the mature cells. It is particularly significant in consideration of this possibility that auxin is acid in reaction. When the cells are too far removed from the source of auxin and the electrical potential difference between the nucleus and the cytoplasm of mature cells is small, and the "trigger energy" is spent, a state of equilibrium is produced, so that the activity of the cell is nearly purely physical and the osmotic quantities are more involved in the functioning of older cells than in the younger.

These notions are helpful to a better understanding of the evident correlation of cell proliferation and cell enlargement, the evident dependence of

both on mitosis, and the influence of the chromatin on the phenomena accompanying growth. They also help to make it clear that the nucleus is indispensable for the physiological activity of the cell in general, and growth by cell enlargement in particular. It is suggested accordingly that the natural auxin has its source in the nucleic acids and depends on the mitotic activity for its production. Also that its bio-regulating effect depends upon its power to direct the formation of specific asymmetric structures within the protoplasm and that this effect is inductive and need not necessarily be conducted to exercise its influence. The induction might well occur electro-magnetically. This view receives encouragement from the fact that so many different kinds of organic acids can exercise an effect similar to that of auxin upon plant cells. It is doubtful if these acid agents produce exactly the same physiological effect as does the natural auxin, but their acid nature can influence the protoplasm in such a manner that growth by cell enlargement is simulated.

THE OSMOTIC VALUE AND THE EQUIVALENT SUCTION TENSION OF THE CELL SAP OF CELLS IN THE NORMAL, PLASMOLYZED, AND SATURATED STATES

The concentration of the sap, which contains organic and inorganic solutes, is not the same for a given cell in the normal, plasmolyzed, and saturated states. The concentrations in the three states are symbolized by (O_n), (O_g), and (O_s), respectively, and are expressed numerically in function of the concentration of the plasmolyte which has the same osmotic pressure. The suction tensions which are equivalent to the concentrations (O_n), (O_g), and (O_s) are symbolized by (Si_n), (Si_g), and (Si_s), respectively, and are expressed in atmospheres.

It is evident from the nature of the process employed that for a given cell or tissue:

$$O_g > O_n > O_s; \text{ and}$$
$$Si_g > Si_n > Si_s.$$

This fact is well illustrated by our recorded results (see table 2).

Weber (51, 52) pointed out that the normal permeability of the protoplasm is changed by plasmolysis when certain plasmolytes are employed. He speaks of "plasmolysis permeability." He and Strugger (42) agree with Beck (2) that when sucrose is employed as a plasmolyzing agent there is no immediate influence exerted upon the permeability of the protoplasm. Our experience in the present work is in accord with this view.

The time necessary to produce incipient plasmolysis was found to be greater for young cells than for older cells. This became particularly evident when, after a number of trials, the concentration which produced incipient plasmolysis was determined, and then fresh tissue was placed in the sugar solution of that concentration, which was approximately the correct O_g

value, and the time required to produce plasmolysis was determined. We did not go into this matter as thoroughly as others, but we can safely state that young cells required more time to become plasmolyzed than did mature cells. When excessively high concentrations were employed, the protoplasts of the young cells became plasmolyzed in a shorter time than in the nearly correct O_g concentration, but the form of the plasmolyzed protoplasts was not convex, as it normally should have been. If sufficient time was allowed, however, the "cramped plasmolysis" form, as Weber calls it, changed to the normal convex form. This fact indicates that the protoplast of young cells is more viscous than that of mature cells. It is also evidence that the protoplasm of young developing cells is in intimate union with the cell wall and in the process of plasmolysis is torn away violently at many points, but remains

TABLE 2. *The Concentration and the Suction Tension of the Cell Sap in the Normal, Plasmolyzed, and Saturated States, Expressed in Mols and Atmos., Respectively.*

Zone	At Incipient Plasmolysis				In the Normal State				In the Saturated State			
	Epidermis		Cortex		Epidermis		Cortex		Epidermis		Cortex	
	O_g	Si_g	O_g	Si_g	O_n	Si_n	O_n	Si_n	O_s	Si_s	O_s	Si_s
1	0.28	7.6	0.407	11.41	0.27	7.3	0.405	11.35	0.268	7.24	0.362	10.06
2	0.255	6.8	0.40	11.20	0.248	6.64	0.398	11.14	0.233	6.29	0.360	10.00
3	0.25	6.7	0.385	10.75	0.243	6.49	0.384	10.72	0.241	6.43	0.342	9.46
4	0.24	6.4	0.345	9.55	0.288	6.14	0.344	9.52	0.226	6.08	0.309	8.47
5	0.23	6.2	0.340	9.40	0.225	6.05	0.339	9.37	0.221	5.93	0.312	8.56
6	0.23	6.2	0.310	8.50	0.266	6.08	0.309	8.47	0.244	6.02	0.302	8.26
7	0.23	6.2	0.295	8.05	0.266	6.08	0.294	8.02	0.225	6.05	0.284	7.72

attached at some points. These facts suggest that in careful work in which the plasmolytic method is employed, the final readings should be determined with solutions which are not far removed from the true O_g concentration, and sufficient length of time should be allowed for evident convex plasmolysis. These precautions were taken in our work, and we feel certain that the protoplast was not injured as the result of violent treatment. We found that mature cells usually did not require more than ten minutes to plasmolyze but young cells sometimes required thirty minutes.

Since, as was previously described, the volumes of the cells at incipient plasmolysis, in the normal state, and in the saturated state are known, it is not difficult to calculate the concentrations of the sap in the normal and saturated states from the concentration in the state of incipient plasmolysis by the methods described by Ursprung (45). The equivalent suction tensions can be obtained from the table of Ursprung (45) in which the equivalent concentrations and osmotic pressures are listed for sucrose. The results which we obtained are given in table 2.

The Osmotic Value at Incipient Plasmolysis. This quantity expresses the concentration of the sap when the protoplast has slightly receded from

the cell wall in consequence of the contraction produced in it by exosmosis after having been placed in a hypertonic sugar solution. When the value is expressed for a tissue it is understood that fifty per cent of the cells are in the state of incipient plasmolysis.

Normally the semipermeable protoplast is in contact with the cell wall, which is permeable. When the protoplast is distended by the hydrostatic pressure within, it usually presses against the cell wall with sufficient force to distend the cell wall, providing the wall is not too rigid. If the internal pressure is relieved, not only does the protoplast contract but also the distended wall. Evidently a rigid wall will not contract, nor will a plastic wall which is devoid of all elasticity. An elastic wall will contract to a degree commensurate with its degree of elasticity. From these considerations it becomes clear at once that the capacity of the mature cell does not differ much from its capacity in the state of plasmolysis if the wall is rigid because the protoplast leaves the wall as soon as it begins to contract. The plastic walls of young cells, such as those in the first and second zones of our plants, do not recede much because they lack elasticity. It follows that cells with elastic walls manifest a greater difference between O_n and O_g than do cells with rigid walls or such cells that have plastic walls which are readily stretched beyond the limits of elasticity. Even though the value $O_g - O_n$ can give some indication of the nature of the wall, an exact expression cannot be expected because the capacities of the normal cells in the different zones are not comparable. Our O_g and O_n data approximately indicate that both the epidermis and the cortical tissues are most elastic in the third and fourth zones.

In our present study the osmotic value at incipient plasmolysis is of little value in determining the physiological effects of growth in the various zones because of the excessive number of variables which are involved; this fact makes comparisons practically impossible. This does not, of course, mean that in general, all other things being equal, the O_g variations cannot serve as indicators of the variation in the physiological activity of the protoplast in response to external factors. As Beck (4, 5) showed, the O_g is appreciably affected by certain external factors which indicate a physiological reaction in the protoplast.

The values which we obtained for the cortical tissue are consistently lower than those given by Ruge for the same tissue. The lack of light and relatively high humidity conditions which prevailed constantly in our experiments (but not in Ruge's) tend to lower the O_g, so that the order of our data is as might be expected.

Beck (5) showed that the tissues of herbaceous plants have lower O_g values than do woody plants. The relatively low values which we obtained in the present experiments are in accord with this fact. The average values,

0.244 mol. for the epidermis and 0.354 mol. in the cortical region, are just what might be expected in tender sunflower seedlings grown under the given conditions.

O_g for the epidermis in zone 1 (0.28 mol.) is high compared with the value for zone 2 (0.25 mol.). Many trials gave this high value consistently. The embryonic state of many of the cells of zone 1 account for this. In this zone the youngest cells plasmolyze with difficulty because the cell sap cavity is small and the water uptake in the embryonic and slightly developed cells is mostly due to the imbibition of the protoplasm itself.

When an attempt is made to plasmolyze very young cells a plasmolyte of relatively high osmotic pressure must be employed to overcome the imbibition of the protoplasm so that the value obtained for zone 1, which is an average expression for the entire zone, includes the results obtained with embryonic cells which cannot have a true osmotic value and young cells having a small vacuole in which the protoplasm still has a high degree of imbition.[3] Thus it is clear that the value (0.28 mol.) which was obtained by the methods which are legitimate for older cells, but not entirely reliable for very young cells, is naturally relatively high but involves forces that are non-osmotic in nature. The same may be said for the cortical cells in which the O_g for zone 1 was 0.407 mol.

The O_g gradient in both the epidermal and cortical tissue is in the direction of the movement of the water in the plant. The difference between the values of the oldest and youngest cortical cells is greater than the difference for the corresponding epidermal cells (see table 2 and figure 3). It may be thought that gradients similar to the one found in our seedlings must necessarily exist in all plants. It is, however, a fact that many authors give data for various kinds of plants, where the O_g gradient is not in the direction of the streaming of the water in the plant. The data as given by them are, no doubt, correct and not difficult to understand when it is remembered that it is not the O_g gradient which decides the direction in which the water shall flow, but the gradient of the suction tension of the cell (Sz_n).

It must, furthermore, be remembered that it is not to be concluded from the data given in table 2 that the O_g of the older tissues is low because the normal influx of water was greater than the amount of solute which was produced during the process of cell development, because Beck (10) showed that in epidermal cells of strictly comparable plants the production of solute is directly proportional to the growth of the cells. Beck, Lonsing, and Andrus (14) showed, in strictly comparable plants, that this is also true for the cortical cells. It follows that the lower O_g value in the older cells cannot be ascribed to a lack of the production of solutes, but must rather be ascribed

[3] In this connection the experience of Weber (52) and Strugger (42) should be recalled. They proved that the viscosity and imbibition pressure is maximum in the youngest cells and decreases as the cells develop.

to the increased capacity of the older cells and the changed conditions of the cell wall, particularly its increased rigidity.

Beck (5) showed in tests which he made on many plants that the O_g of the epidermis is always lower than the O_g of tissues that lie within. Our figures are in accord with this fact. The difference between the O_g values found for the cortical and epidermal tissues is greater in young zones than in mature zones (see figure 3). These results indicate that in general the

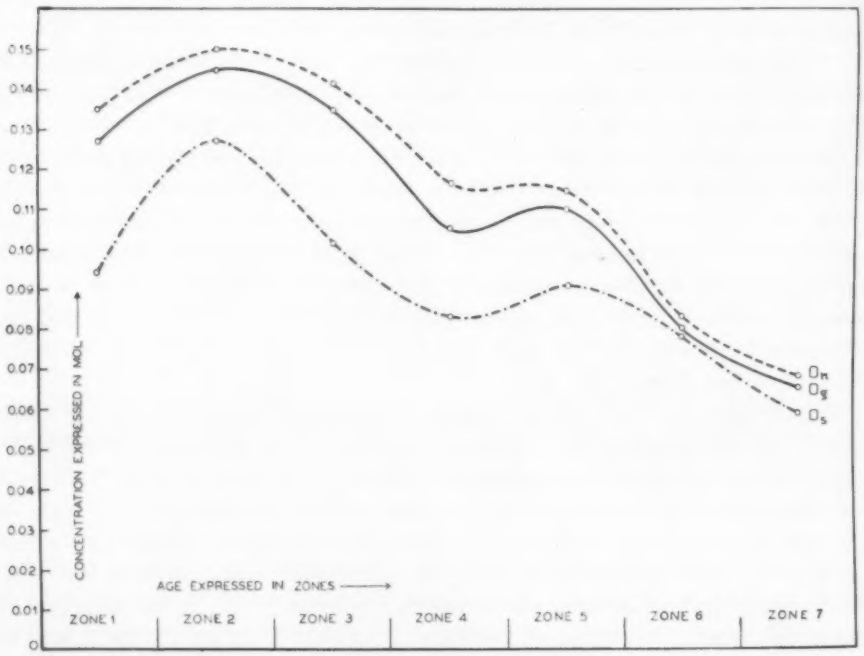

FIG. 3. Difference between the epidermal and cortical sap concentrations: O_g, O_m, O_s, correlated with the age of the tissues.

cortical cells can change their volume considerably more than the epidermal cells can during the process of plasmolysis, at least in the first five zones. This would indicate that the cortical tissue is a more dynamic tissue than is the epidermis. No doubt, the fact that relatively more solute is produced in the cortical tissue than is produced in the epidermis, is also a factor which must be borne in mind in comparing the O_g values for the two tissues. As a matter of fact the thickness of the wall is greater in the older epidermal cells than it is in the older cortical cells. In this connection it is interesting to note that in zone 3 the hypocotyl takes on an opalescent appearance, while in zones 1 and 2 the general appearance is more waxlike. The opalescence is, no doubt, the result of the total reflection of light caused by the intercellular spaces of the cortical tissue that are formed, as the result of the hydrostatic

pressure of the individual, cylindrical cortical cells, which are only in tangential contact. This may be taken as an indication of the dynamism of the cortical tissue.

Concentration of the Normal Cell Sap (O_n). This quantity expresses the concentration of the cell sap as it actually occurs in the plant at the time when the tests are made. It is symbolized by O_n and is expressed in molar concentration. It must not be confused with the osmotic value at incipient plasmolysis. This value can change rapidly in response to external factors without necessarily suffering a change in the amount of solute which is present. In the particular experiments under consideration such fluctuation in response to external factors did not occur, because all the plants employed were strictly comparable and the external factors which might influence the concentration of the sap were carefully controlled and were approximately constant. The results obtained are in table 2.

The suction tension of the contents of the cell in the normal state (Si_n) expresses the negative physical pressure which is caused by the osmotic virtue of the solutes contained in the cell sap. Like all other suction tensions it is expressed in atmospheres. The equivalent concentration is the osmotic value of the sap in the normal state, and is expressed in mols; it is symbolized by O_n. Since both the concentration and the suction tension of the sap in the normal state are useful in the comparisons and discussions for the seven zones of the hypocotyl of *Helianthus* seedlings they have been arranged in table 3.

TABLE 3. *Suction Tension (Si_n) and Equivalent Concentration of the Cell Sap (O_n) in the Normal State for Helianthus Seedlings.*

Zone	Epidermis		Cortical		Tab. Diff. of (Si_n)
	(Si_n) in Atmospheres	(O_n) in Mol.	(Si_n) in Atmospheres	(O_n) in Mol.	
1	7.3	0.270	11.35	0.405	4.05
2	6.64	0.248	11.14	0.398	4.50
3	6.49	0.243	10.72	0.384	4.23
4	6.14	0.228	9.52	0.344	3.38
5	6.05	0.225	9.37	0.339	3.32
6	6.08	0.226	8.47	0.309	2.39
7	6.08	0.226	8.02	0.294	1.94

The normal suction tension of the cell as an entity (Sz_n) is not given by the value Si_n because the wall pressure, and possibly some other vectors, tend to prevent an influx of water into the cell induced by the vector Si_n. Si_n and Sz_n differ in scalar value but not in direction. The two quantities usually vary in the same way.

The suction tension of the normal cell sap and the hydrostatic pressure produced by the influx of water into the cell sap cavity affect the state of the

protoplasm. It is well known that the protoplasm of aging animal tissues loses water just as do hydrophilic colloids. In gels the time factor is especially apparent. It cannot be concluded from this, however, that the cell sap of developing plant cells is the result of the aging of the protoplasm in these cells. The protoplasm of aging animal tissues increases in viscosity, but in the protoplasm of plant cells, which grow by cell enlargement, the viscosity decreases. For a review of the literature on this subject the reader is referred to Strugger (42). Strugger proved conclusively and gave experimental evidence that the plasmatic characteristics are distributed in a regular manner in the form of a plasmatic gradient in leaves, roots, and shoots, and that these characteristics can be immediately correlated with the physiological zoning. The plasmatic differences of the cells in the process of enlargement consists in the significantly higher degree of viscosity of the protoplasm in the growing cells in comparison with viscosity of that of the mature cells (42; see also Weber, 48).

The production of solute must be regarded as an active physiological process concomitant with other growth phenomena induced by auxin. Beck (10) and Beck, Lonsing, and Andrus (14) showed that in developing cells of the hypocotyl of *Helianthus* seedlings the production of solute in growing cells is proportional to the growth.

These findings indicate that the water which is available for the active protoplasm is of great importance for its optimum physiological activity. The amount of water which may be withdrawn from the protoplasm without serious injury is limited. An excessive supply of water, which may be regarded as waterlogging, is not favorable for the physiological activity of the protoplasm, as was shown by Beck (11). The O_n represents the concentration of the cell sap which is in equilibrium with the active normal protoplasm.

It follows from these considerations that a knowledge of the O_n should prove to be valuable, not only for our present purpose, but also for future comparisons and studies regarding the physiological activity of developing cells.

Rapid variations of the O_n may not, however, be taken as indicators of physiological activities because changes in O_n due to external factors occur very quickly and are largely due to purely physical forces. In our experiments there were no such rapid changes either in the O_n or in the factors of the environment.

Many of the data given in the literature for O_n (sometimes confused with the quantity O_g) were obtained by cryoscopic methods. Such data must be recorded as average values for tissue complexes, organs, or entire plants, and are of little value in discussions regarding changes in the cells during their development. The data of Ursprung and Blum and of others who followed their lead in the study of osmotic quantities give Si_n values for individual

cells and averages for tissues obtained by calculation from direct plasmolytic determinations. These data are better adapted for comparative studies. Our data, given in table 3, express the average value for the cortical and epidermal tissues in the respective zones as indicated. Since they were obtained by the plasmolytic methods according to the direction of Ursprung and Blum, and since the factors of the environment were controlled and all plants were strictly comparable, they can serve to indicate changes in the state of the growing tissues.

The values for O_n given in table 3 are relatively low when compared with values of similar tissues given in the literature for mature plants. This is not surprising because the young seedlings were grown in light sandy, moist, soil, and in air of high relative humidity at optimum temperature. It is well known that external factors in general influence the O_n and the Si_n. Air of low relative humidity, dry soils, and temperatures varying greatly from 25° C tend to increase these quantities (4, 44).

There is an almost regular but not sharp gradient extending from the oldest cells in the seventh zone to the youngest in the first zone of the epidermis. A similar, but even sharper gradient is evident in the cortical tissue. The Si_n gradients are, of course, similar to the O_n gradients and the numerical expression of the quantity in atmospheres makes the gradient more pronounced (7.3–6.08 atmos. and 11.35–8.02 atmos. respectively; see table 3). It cannot be concluded legitimately that such O_n gradients in the flow of water in the plant must necessarily exist because it is not the quantity Si_n but rather the quantity Sz_n which decides in which direction the water will flow.

The values of Si_n and O_n are consistently higher in the cortical tissue than they are in the epidermal tissue. The differences are given in the last column of table 3 (see also figure 3). These differences show clearly that there is an Si_n gradient and an O_n gradient radially from the epidermis to the cortical tissue. These gradients must not be regarded as proofs that the water will necessarily move from the epidermis to the cortical tissue, since the Si_n and O_n differences are not satisfactory indicators of a difference of potential between any two cells or tissues. As stated above, it is the Sz_n gradient which is the deciding factor for the direction of the flow of water. Other things being equal, however, the gradient as we find it favors a similar gradient for the suction tension of the cell Sz_n and tends to cause a flow of water from the epidermis to the cortical tissue. These findings, therefore, are in harmony with the view that the epidermis tends to serve as a water reservoir. In general the values obtained favor the notion that the water flows upward in both tissues and inward from the epidermis to the cortex. The difference between the suction tension of the sap of the two tissues is considerably greater in the youngest zone (zone 1) than it is in the oldest zone (zone 7); 4.05 atmos.–1.94 atmos. (see table 3). This great difference does not

imply that the difference is equally great for the suction tension of the two tissues. Later, attention will be drawn to the fact that the figures for the suction tension of the sap and the suction tension of the tissues are of the same order, but not of the same magnitude, and that the difference between the suction tension of the cortical tissues and the epidermal tissues of the youngest zones and of the oldest zones is actually considerably less (5.8 atmos.–4.2 atmos.; see table 4) than it is in the present case for the suction tensions of the sap in the same tissues. This indicates that the wall pressure in these two zones has changed considerably in the process of growth.

The Concentration of the Sap When the Cell is Saturated with Water (O_s). This quantity expresses the concentration of the sap when the cell has been permitted to take in all the water possible, while being immersed in water. It is symbolized by O_s and is expressed in molar concentration.

A considerable difference between O_n and O_s would indicate that much water can be absorbed by the normal cell when thus immersed, i.e. the suction tension of the cell is not rapidly reduced by the influx of water, or in other words a counter-pressure is not rapidly set up during the influx of water. From this it follows that under such conditions the cell wall does not develop an appreciable wall pressure as the result of expansion by the hydrostatic pressure.

When the difference ($O_n - O_s$) is not great it may be because the capacities of the cells are large and the plant in the normal state can take up water without considerable reduction of the concentration of the cell sap. In the present experiments the difference is small and the conditions are such that both tissues in the normal state are almost saturated. One may not use the difference $O_n - O_s$ as a basis of judgment regarding the elasticity of the cell walls without risk of error.

The results indicate that both the cortical and epidermal tissues are more plastic in the first and second zones and more rigid in the sixth and seventh.

The differences between the concentrations of the sap in all three states becomes less with age. In the mature zones the differences between the concentrations for the sap in the two tissues in the three states are all nearly the same (see figure 3). This is, no doubt, due to the increased rigidity of the wall in both tissues. These differences of concentration in the two tissues are always least for the O_s and greatest for the O_n.

It should be remarked here that the value Si_s is numerically equal to the wall pressure W_s, since the action and reaction are equal and opposite in direction when the gorged cell is in a state of equilibrium and the wall pressure upon the protoplast and vacuome prevents the further influx of water.

SUCTION TENSION OF THE CELL IN THE NORMAL STATE (Sz_n)

Since the suction tension of the cell, as an entity (Sz_n), is the result of the suction tension of the contents of the cell (a vector acting in one direc-

tion) and the wall pressure (an antagonistic vector), important conclusions regarding the nature of the wall in growing regions can be arrived at from a knowledge of this osmotic quantity for cells in various phases of growth. Physical changes in the growing cell wall produce definite effects upon the force which tends to cause water to flow into a cell, even though the wall itself is pervious to water and does not prevent the water system from being continuous from one cell sap cavity to another, through the membranes and the protoplasm itself.

This quantity (Sz_n) expresses the force per unit area with which the cell as a whole tends to draw water into itself, either from a direct source of water or from some neighboring cell which has less tension. It is not our purpose to determine at this time whether the cell is active or passive in this process of water intake, but merely to determine the vector value which tends to produce a state of equilibrium.

The numerical expression of this quantity (Sz_n) is a good indicator of the tendency of water to flow in one or the other direction: from the environmental cells to a given cell or in the reverse direction. In the present study we are not considering the suction tension of individual cells but the average Sz_n of the cell complex in a section of a given tissue as determined by the simplified method of Ursprung (45). This average value will indicate the general direction of the flow of water.

The numerical expression of this quantity can be determined directly and can also be calculated from the known osmotic pressure of the normal cell sap which is numerically identical with the suction tension of the sap in the normal state, and the known wall pressure which tends to press water from the cell, according to the law of Ursprung as expressed in the equation:

$$Sz_n = Si_n - W_n \qquad (1)$$

in which Sz_n is the suction tension of the cell; Si_n, the suction tension of the contents of the cell; and W_n, the wall pressure.[4]

In the present work the values for the epidermal and cortical tissues in various zones of the hypocotyl of *Helianthus* seedlings were determined

[4] Here no account is taken of vectors other than that of the wall pressure which tends to reduce the suction tension of the cell, such as the tension or pressure of neighboring tissues. The complete equation is:

$$Sz_n = Si_n - (W \pm A) \qquad (2)$$

in which A represents the additional forces such as tissue tension, besides the wall pressure which tends to increase or decrease the suction tension of the cell.

It would, of course, have been most desirable to have determined the term A, particularly for the pressure produced by the epidermal tissue upon the cortical in the normal hypocotyl, but we were unable to devise a method to do so. In the interpretation of the results this must be borne in mind that our results refer to the suction tension of an excised group of cells in which the counter-pressure of the epidermis upon the cortical tissue was necessarily disregarded. In spite of the difficulty of not being able to obtain more than an approximation of the suction tension of the cells in the normal state, the data are very enlightening.

directly and also by calculation, and the results have been recorded in table 4. The symbol Sz_n is employed to express this average value of the tissue even though it strictly refers to individual cells. In order to determine the suction tension directly by experiments some authors keep the same test strip and place it in different concentrations of the plasmolyte and note in which concentration the strip maintains its original length. The osmotic pressure of that concentration is accepted as the suction tension of the sample. This method is satisfactory if the wall is elastic and is not stretched beyond the limits of elasticity. Since we have evidence that the walls of young cells of the hypocotyl in question are not elastic but plastic, it was not safe to employ this method. We therefore never carried a test strip from one concentration to another. A fresh sample was taken for every concentration employed. After preliminary tests indicated the upper and lower limits of the Sz_n value, with but slight variation, final tests were made in graded solutions, which did not vary much from each other and were within the limits found in the preliminary tests. The osmotic pressure of the concentration, in which the sizes of the cells did not vary from the original, was accepted as the Sz_n of the cells tested.

TABLE 4. *Suction Tension of the Cells (Sz_n) in the Epidermal and Cortical Tissues of Helianthus Seedlings.*

Zone	(Sz_n) in Atmospheres				Diff. of (Sz_n) of the Tissues	
	Epidermis		Cortical			
	Exp. Data	Cal. Data	Exp. Data	Cal. Data	Exp. Data	Cal. Data
1	5.3	5.17	11.115	11.093	5.815	5.923
2	5.2	5.24	10.930	10.796	5.730	5.556
3	5.1	5.17	10.600	10.583	5.100	5.413
4	4.9	5.02	9.40	9.265	4.50	4.235
5	4.0	3.92	8.95	9.015	4.95	5.095
6	3.7	3.80	8.20	8.30	4.50	4.50
7	3.4	3.68	7.60	7.630	4.20	3.95

An Sz_n gradient in the direction of the flow of water in a plant, as for example from the roots to the leaves, was long suspected and was finally proven to exist by Ursprung and Blum (43, 44, 47) and others. A study of the nature of the suction tension of the cells makes it evident that such a gradient must exist. If there was ever any doubt about it because of data obtained by cryoscopic methods, it is the result of confusing the quantities, suction tension of the contents of the cell (Si_n), which is numerically identical with the osmotic pressure of the normal cell sap, and the suction tension of the cell (Sz_n). An Si_n gradient in the direction of the flow of water in the plant may exist in a given instance as in our present experiments (see table

3) but in general need not exist. An Sz_n gradient from the oldest cells to the youngest in both tissues is evident and not surprising.[5]

In the epidermis the greatest variation from the average potential difference is between zones 4 and 5 (0.9 atmos.). The greatest variation from the average potential difference in the cortical tissue occurs between zones 3 and 4, namely 1.2 atmos. These greater differences must be interpreted to mean that either critical changes in the nature of the cell walls occur in the hypocotyl between 15 mm. and 25 mm. from the base of the cotyledons, or changes in solute production, or both. Apparently the changes occur somewhat earlier in the cortical tissue (third and fourth zones) than in the epidermis (from the fourth to the fifth zone). Since the amount of solute production is proportional to the growth in both tissues (10, 14), it follows that the high potential difference must be due to changes in the wall, rather than to irregular solute production; and since the enlargement of cells is regular, these relatively sudden changes in suction tension can only be interpreted as due to changes in the wall pressure, and consequently changes in the nature of the wall.

The difference between the suction tension of the epidermal and cortical tissues is considerable, the average being approximately 5 atmospheres. It is somewhat greater than the average in the youngest three zones and somewhat less in the oldest four zones. If the physical pressure imposed upon the cortical tissue is disregarded, these figures would indicate that the water tends to flow from the epidermis to the cortical tissue, which is in harmony with the notion that the epidermal tissue serves as a water reservoir. The fact that the difference is less in the older zones and greater in the younger would seem to indicate that the flow of water from the epidermal tissue to the cortical tissue occurs more readily in the younger zones. It would thus appear that the young developing cortical cells, not far removed from the region of proliferation, can be quickly supplied with water from the older cortical cells and also from the epidermal cells of the same age.

The high average difference between the two tissues must not be interpreted to mean that the possible flow of water from the epidermis to the cortical tissue is necessarily great, because the nature of the walls of the two tissues is not the same, and it is quite possible that a sufficient resistance is offered by the walls to reduce the water current which is induced by the high potential difference of 5 atmospheres. If it were possible to determine the resistance of the wall to the flow of water and incorporate it in the gen-

[5] Experimental evidence of the correctness of the interpretation, that is of the flow of sap as indicated by the gradient, was obtained by administering sugar solutions of slightly greater osmotic pressure than the recorded suction tension of the cells in the uppermost zones, and it was noted that the hypocotyls wilted; the wilting being noted first directly above the soil, and then it progressed steadily to the uppermost zone. These facts indicate that the flow of water was reversed, passing from the upper zones to the next lower zones.

eral equation (2) as a part of the term A, the final potential difference between the two tissues would undoubtedly be less than 5 atmospheres.

The average potential difference between the epidermal cells from zone to zone is only 0.3 atmosphere, whereas the difference from epidermal tissue to cortical tissue is approximately 5 atmospheres. This is rather surprising, since the potential difference vertically must be sufficient to cause the water to ascend against the force of gravity and also to overcome the resistance of the horizontal cell walls. It is difficult to see how the water could rise in the epidermal cells unless a wall resistance to the flow of water from the epidermis to the cortical tissue is assumed. This assumption would presuppose that the nature of the vertical walls of the epidermal tissue is different from the horizontal walls of the epidermal cells. This assumption is not too bold in view of the fact that it is well known that cell walls do not grow much horizontally, but do grow vertically (17). We might then well assume that the vertical walls offer a great resistance to the flow of water, but the horizontal walls offer less resistance, so that the water flows more readily vertically into a given epidermal cell than it does from the same cell horizontally, in spite of the greater horizontal potential difference. It may further be assumed that the wall resistance to water flow from epidermal tissue to cortical tissue increases with the development of the cell wall, i.e. it is greatest in mature cells and least in young cells. In the older cells where, as was previously shown the difference between the Si_n values for the two tissues is least and the wall resistance to water flow is probably greatest, there is not so great a tendency of water to flow from the epidermis to the cortical tissue in spite of the potential difference indicated by Sz_n differences (see table 4, col. 6, 7) as there is in the younger cells.

THE WALL PRESSURE AND THE NATURE OF THE WALL

The wall pressure is a vector which acts antagonistically to the hydrostatic pressure and tends to diminish or to prevent entirely the influx of water into the cell sap cavity. When the cell is in the state of incipient plasmolysis its scalar value is evidently zero, but in the saturated state it is maximum, and it is equal to the hydrostatic pressure or to the osmotic pressure of the cell sap (Si_s). Assuming that the increment of the wall pressure, from incipient plasmolysis to the saturated state, is proportional to the change in the volume of the cell, the wall pressure of the normal cell can be determined according to the equation:

$$W_n = W_s \times \frac{V_n - V_g}{V_s - V_g} \qquad (3)$$

in which W_n is the wall pressure in the normal state; W_s, the wall pressure in the saturated state; $(V_n - V_g)$, the change in volume from the normal state to the state of incipient plasmolysis; and $(V_s - V_g)$, the change in volume from the state of plasmolysis to the state of saturation.

From the formula it is evident that the contraction and the expansion of the cell wall are important factors which influence the value W_n. If the cell wall is extensible it offers little resistance, so that $V_s - V_g$ is relatively great and the value of W_n is proportionately small; furthermore, under this condition the influx of water is relatively great and the osmotic pressure (which is numerically equal to W_s) of the cell sap at saturation is correspondingly low, so that both factors tend to make W_n relatively low when the walls are plastic and extensible. If the walls are not plastic, but elastic, $V_s - V_g$ becomes less, W_s becomes greater and W_n becomes greater in consequence. The rate of increment will depend upon the coefficient of elasticity of the cell wall. When the walls are rigid, or only slightly elastic $V_s - V_g$ is small, and W_s not much different from Si_g, i.e. relatively high. In consequence W_n is great and the rate of increment from zero to maximum is great.

From these considerations it is evident that the values obtained for W_n should indicate, to some extent at least, the nature of the cell walls in the various stages of cell development; but W_s depends also upon the capacity of the cell and on the solute produced during the cell's growth, it may not be assumed that the variations of W_n give an exact expression of the variations of the modulus of elasticity of the wall.

In this connection it should be recalled that the discovery by Ursprung and Blum (47) that turgor was minimum in the zones of vigorous growth created surprise only because the nature of the osmotic quantities and the nature of growth by cell enlargement were so little understood at the time. Now that the osmotic relations are better understood and our knowledge of the structure of the cell wall in the various stages of the cell's development has advanced their results appear to be as they should be, and the old and widely held view that cell enlargement is entirely due to the hydrostatic pressure from within is untenable.

These facts must be borne in mind during the interpretation of our results. While it cannot be claimed that the wall pressure gives quantitative expression of the plasticity, the rigidity, or the coefficient of elasticity, nevertheless the results give some evidence of the condition of the wall in the various stages of the development of the cell, and are not contradictory to the known facts regarding it.

Ursprung and Blum's discovery of minimum turgor in the zone of maximum growth gave the first experimental evidence that the wall must grow actively during the process of growth by cell enlargement. The reader is referred to the reviews of the literature on this subject by Frey-Wyssling (21) and by Anderson (1). Undoubtedly the biochemical regulator auxin induces the active growth of the cell wall, but with time it is becoming more evident that the material added to the wall is elaborated by the protoplast. Not only is the mass of the wall changed during growth but its nature also;

the extensibility, the elasticity, and the rigidity are all modified. Heyn (28) and Söding (39) produced conclusive evidence that the changes in the nature of the cell wall are not, however, primary causes of growth. Gessner (23) also showed that a change in extensibility must be considered a phenomenon of growth and not its cause. The data which we present are not intended to prove these facts, but they are in agreement with them and serve well to illustrate them.

In table 5, the results obtained for W_n are given for the two tissues. Considerable experimental error was discovered in our data for the cortical tissue in the sixth zone and conditions prevented a repetition of the experiment so that the space for that value was left blank.

In the examination of our data it must not be forgotten that although the hydrostatic pressure is not the cause of growth, it is, like the increment in the wall and the changes in the wall's nature, a growth phenomenon. Unless solute were produced as cell enlargement proceeds the turgor could not well be maintained. As previously stated Beck, Lonsing, and Andrus (10, 14) proved that the production of solute is proportional to the growth. The importance of the solute as a factor in the production of wall pressure is evident from the equation:

$$W_n = Si_n - Sz_n \qquad (1)$$

in which W_n is the wall pressure; Si_n, the suction tension of the contents of the cell; and Sz_n the suction tension of the cell as an entity. From a comparison of the Si_n values given in table 3, the Sz_n values given in table 4, and the W_n values given in table 5, it becomes evident that the relatively low Sz_n values for both tissues in the growing zones are undoubtedly determined by the changes in the nature of the wall rather than by changes in the rate of solute production. To make this more evident these different values have been plotted against the distance from the cotyledons (see figure 5). If the cell were not to change its volume and if the nature of the wall were to remain the same, the maximum (Sz_n) and the minimum turgor in the region of greatest growth could not be explained because the turgor should in that case increase proportionately with the solute production. This, however, not being the case, the changes in the wall must be assumed actually to occur. The changes might be in the volume of the cell, or in the nature of the cell wall, or in both.

In table 5, the normal wall pressure and the pressure of the saturated cell are recorded. The normal wall pressure is given as derived from equation (1) in which Sz_n was obtained by direct experiment and Si_n as previously explained. It is also given as obtained by calculation according to equation (2). For both tissues the results obtained by the two methods are of the same order and of nearly the same value.

The W_s is recorded only for the purpose of giving the quantities necessary for checking the results. As previously explained they represent the

osmotic pressure of the cell sap at the point of saturation. Since the forces involved are not purely osmotic in the first zone and to some extent in the second, the actual W_s is probably lower than the recorded value. Since W_s is an implicit function in equation (3) the value of the explicit function W_n must be too high for these two zones. The results obtained by equation (1) (in which W_s is not involved) can be considered as being obtained by direct experiment. They are actually somewhat lower than those obtained by equation (2). They are, nevertheless, too great, because the values Si_n and Sz_n also involve non-osmotic forces in these two zones. We have no means of determining exactly how much lower the two values actually are. The fact

TABLE 5. *The Wall Pressure of the Developing Epidermal and Cortical Cells in the Hypocotyl of Helianthus Seedlings in the Normal State (W_n) and in the Saturated State (W_s).*

Zone	(W_n)				(W_s)	
	Epidermis		Cortical		Epidermis	Cortical
	Derived from Equation $Si_n - Sz_n = W_n$	Calculated from Equation $W_n = W_s \times \frac{V_n - V_g}{V_s - V_g}$	Derived from Equation $Si_n - Sz_n = W_n$	Calculated from Equation $W_n = W_s \times \frac{V_n - V_g}{V_s - V_g}$	Experimental	Experimental
1	2.0	2.13	0.235	0.257	7.24	10.06
2	1.44	1.4	0.210	0.344	6.29	10.00
3	1.39	1.22	0.120	0.137	6.43	9.46
4	1.14	1.12	0.120	0.255	6.08	8.47
5	2.05	2.03	0.42	0.355	5.93	8.56
6	2.28	2.18			6.02	8.26
7	2.58	2.4	0.42	0.390	6.05	7.72

that we failed to obtain minimum turgor at the point of maximum rate of enlargement, i.e. 6.5 mm. from the base of the cotyledons or in the uppermost region of the second zone (10, 14), is, no doubt, due to the involvement of non-osmotic forces. Our actual minimum occurred in the fourth zone. This is particularly interesting because previously Beck and Donnelly (13) established the fact that in strictly comparable plants a critical point occurs beyond which the cells respond with great difficulty to geotropic stimulation. The point is well defined and is located 25 mm. from the base of the cotyledons, or at the end of the fifth zone. Our results and those of Beck and Donnelly clearly indicate that some critical change must occur in the nature of the cell walls which is initiated in the fourth zone and is almost completed in the fifth. If it be assumed (and the assumption is in harmony with our results) that beyond the fourth zone the cells become rigid, the reason for the sharp point of demarcation is given. In the lowermost four zones the

steady increment of the wall pressure is very evident; this is, no doubt, due to the increasing rigidity of the wall. This becomes more evident when it is borne in mind that it is precisely in this region that the ability of the cells to expand when gorged with water (see figure 2) and the change in concentration of the sap from O_n to O_s or $O_n - O_s$ becomes less (see table 2). From these results and considerations it follows that if Ursprung's statement, that the turgor is minimum when the growth rate is maximum, must be taken as strictly correct, it cannot be arrived at by purely plasmolytic methods such as we employed. According to our data the minimum turgor does not occur in a sharply defined manner, so that low turgor extends through the second, third, and fourth zones. The actual minimum is in the fourth zone for the epidermis and in the third for the cortical tissue.

The Modulus. The variations in the wall pressure indicated changes in the physical nature of the cell wall. It is desirable to express such changes in the variation of a modulus. This is, however, always difficult, if at all possible. The volume modulus expresses the restoring force which is evoked by a given change in the mean distance between the molecules, the configuration remaining unchanged. The rigidity modulus measures the restoring force produced by a change in the relative position of the molecules without changing the mean distance. Ordinarily a cross between the two is employed for practical purposes, which is known as Young's modulus. None of these can easily be applied for the interpretation of our data. The data do, however, permit us to express the strain produced by a given stress, and this is what the modulus essentially expresses. It is necessary in the expression of a modulus that the material be not strained beyond the limits of elasticity. Now, our data gave unequivocal evidence that in the first and second zones the turgor stretches the walls beyond the limits of elasticity, so that the figures for these zones might well be questioned. Since it is difficult to verify if the walls have been stretched beyond the limits of elasticity, it is more reliable to employ the figures obtained for the relative contraction rather than those for relative expansion.

In figure 2 the relative expansion and contraction obtained in the various zones for the two tissues is given in graph form. The original sizes were determined while the specimen was immersed in paraffin oil. The expansion was obtained by permitting the cells to gorge themselves with water. The contraction was obtained by placing the specimen in the plasmolyte of the exact O_g concentration.

A study of figure 2 makes it evident that the cortical tissue expands more readily than does the epidermis. In the first four zones it also contracts more readily than the epidermis, but not so in the older zones. In harmony with the conclusion arrived at from the study of the wall pressures these graphs also indicate very evident changes which take place in the nature of the cell

walls, particularly in the third and fourth zones. It was precisely in these zones also where great difficulty was experienced in the exact determinations of the osmotic values by the method of averages and great care had to be exercised. It is now evident that the cells of the fourth zone are in a critical state and difficulty in obtaining consistent results will be experienced if one is not extremely careful to work the determinations exactly at the location within the limits indicated.

Since the cortical tissue expands readily in the first three zones and also contracts to a fair extent (in fact more than in older zones) but not nearly in the same degree as the expansion, it follows that this tissue is plastic but possesses a slight degree of elasticity, and is practically non-rigid, in the first three zones. The epidermal tissue, however, loses in extensibility, but does not lose much in contractibility which would indicate that in the first and second zones this tissue is plastic and is practically non-elastic. The plasticity of the first and second zones can also be detected by attempting to break the hypocotyl in these regions. It breaks very easily under a bending or stretching stress in these zones. Both tissues are therefore practically devoid of elasticity and rigidity in the younger zones. Beyond the fourth zone the hypocotyl is more tenacious and does not break readily under a bending stress or stretching stress.

In table 6 moduli for the various zones are deduced by the equation:

$$M = \frac{W_n}{\frac{L_n - L_g}{L_g}} \tag{4}$$

in which M is the modulus; W_n, the normal wall pressure (stress); and $\left(\frac{L_n - L_g}{L_n}\right)$, the change in length per unit length (strain) from the length at incipient plasmolysis to the normal length.

TABLE 6. *Moduli of the Cell Walls of the Hypocotyl of Helianthus Seedlings.*

ZONES		1	2	3	4	5	6	7
MODULUS EQUATION: $M = \frac{W_n}{\frac{L_n - L_g}{L_g}}$	Epidermis	112.11	134.6	50.6	62.2	81.2	121.1	160.0
	Cortex	16.06	13.23	4.02	13.42	55.5		65.0

In figure 4 the moduli for the two tissues are plotted against the distance from the base of the cotyledons. From this figure it at once becomes evident

that the epidermis in general is more rigid than the cortical tissue and that both tissues begin to become more rigid in the third zone and increase steadily in rigidity up to the maximum in the mature cells. The results are in harmony with the notions that the epidermis is mainly a protective tissue and can serve as a reservoir of water and that the cortical tissue is a dynamic one and readily takes up and gives off water particularly in the younger zones.

FIG. 4. Moduli of the cell walls of the hypocotyl of *Helianthus* seedlings plotted against the age of the cells.

SUMMARY AND CONCLUSIONS

A diagram of the seedlings was made to give the dimensions and show the zones in which the osmotic quantities of the epidermis and cortex were determined. The youngest cells, that is, those of the first and second zones, contained carotinoid pigment but no chlorophyll. These pigments may form a part of the respiratory mechanism and influence the production of auxin.

The determinations of the sizes of the cells proved that they grow by enlargement in the characteristic manner, the maximum rate being at the point 6.5 mm. from the base of the cotyledons, i.e. in the uppermost region of the second zone. The region of cell proliferation does not extend much

beyond 1 mm. from the base of the cotyledons, i.e. the uppermost region of the first zone. The active growth of the walls by intussusception is a fact. Turgor is not the source, or at least not the sole source of energy which causes cell enlargement. The active growth of the wall explains why the minimum turgor exists in the region of maximum growth. The transverse cell walls do not increase their mass appreciably but the lateral walls do. The active growth of the lateral walls, their plastic condition, the high suction tension, and low turgor in the young cells, explain the fact that the hypocotyl is less in diameter in the first zone (see figure 1). Solute is produced in proportion to cell enlargement. The cell sap cavity is small and the forces resembling osmotic forces are really non-osmotic in nature.

The following parallel gradients were established:

1) The plasmatic gradient; maximum viscosity being in the youngest cells.
2) Swelling gradient; greatest swelling power being in the protoplasm of young cells.
3) Electrical potential gradient; the greatest potential being in young cells.
4) Suction tension gradient; maximum suction tension being in the actively growing regions.

There are radial gradients: the concentration of the sap increases from the epidermis to the cortex; the O_g and Sz_n gradients are similar to the Si_n gradient.

The walls of the very young cells are plastic and extensible, while the older ones are less plastic and more elastic, and the mature ones are slightly elastic and almost rigid or non-extensible. All of these effects are probably the result of the activity of the protoplasm which is influenced by the auxin. The auxin need not necessarily be conducted to the protoplasm but may exercise its effects inductively in a physico-chemical manner comparable to the manner in which "evocators" are supposed to operate in animal tissues. It is probable that the chromatin of the young proliferating cells is involved in the process of growth by cell enlargement. The walls of the cortical cells are more extensible than those of the epidermal cells. They are able to contract more than those of the epidermal cells while young, that is, in the uppermost three zones. The walls of the cortical cells are always less rigid than those of the epidermal cells (see figure 4). A critical change begins to manifest itself in the nature of the walls in the third zone, but it does not create an appreciable change in the normal wall pressure until later, i.e. in the fourth zone (see figures 4, 5) where the rate of change is marked. This change explains the critical point at which quick response to geotropic stimulation ceases, namely 25 mm. from the base of the cotyledons. The concentration of the cell sap is maximum when the size of the cell is minimum, and vice versa. This may not be explained on the basis of increased capacity of the cell alone, because the production of solute is in proportion to the growth. O_g, O_n, and O_s are consistently higher in the cortex (see table 2) but the

difference becomes smaller with the age of the cell. In the mature zones the difference is slight (see figure 3).

The suction tension of the cell as an entity is maximum in the youngest zones and minimum in the mature, so that a gradient in the direction of the flow of water is established. A similar gradient exists from the epidermis to the tissues that lie within. The greatest potential difference between the tissues exists in the youngest cells and it is least in the mature cells. If the resistance which the walls offer to the current strength of the waterflow is disregarded, it appears that the water can flow upward in the epidermis and inward to the cortex. It is probable that the older cell walls offer considerably more resistance to the current than do the young cell walls, so that the inward flow is probably considerably less in the older cells than in the younger ones.

The maximum potential difference in suction tension between cells of the same tissue is between the fourth and fifth zones for the epidermis, and the third and fourth for the cortical tissue. This can be explained by the critical changes which take place in the walls of the cells in the respective regions.

The results recorded for the wall pressure give evidence of the changes in the physical nature of the wall during the process of cell enlargement. The results for the turgor are in general agreement with the claims of Ursprung and Blum that it is minimum in the region of active growth. The minimum is not exactly at the point where the rate of enlargement is maximum (6.5 mm. from the base of the cotyledons) but in the fourth zone where the critical changes in the physical nature of the wall occurs, and where the quick response to geotropic stimulation ceases. The turgor is maximum in the mature cells, where the walls are rigid.

In figure 5 the sizes of the cells (L_n) and the values of the osmotic quantities which are of chief interest, namely, the wall pressure (W_n), the suction tension of the normal cell sap (Si_n), and the suction tension of the cell (Sz_n) were plotted against the age of the cells, to give a summary view of their relationships during the process of enlargement.

A summary of the conditions of the cells and the osmotic quantities in the various zones (see figure 1) can be given as follows:

Zone 1. The diameter of the hypocotyl is minimum. The cells contain carotinoid pigment which might form a part of the respiratory mechanism. The uppermost region, approximately 1 mm. in length is the region of cell proliferation; the cells are compressed in appearance, show mitotic figures and lack a cell sap cavity. In the remaining part of the zone the cells fail to divide and begin to enlarge. The protoplasm of the cells is of maximum viscosity as is its swelling power, and its electrical charge. The cell wall is more intimately united with the protoplasm than in the succeeding zones, and plasmolysis is more difficult and takes a longer time. The walls are plastic

and extensible. The hypocotyl breaks easily under a bending or stretching stress. The forces which tend to supply water are largely non-osmotic in nature. The O_g, O_n, O_s, and Sz_n are maximum for both tissues. The respective differences in these quantities for the two tissues are in favor of the cortex and are maximum in this zone. Water flows readily from the epidermis to the cortex.

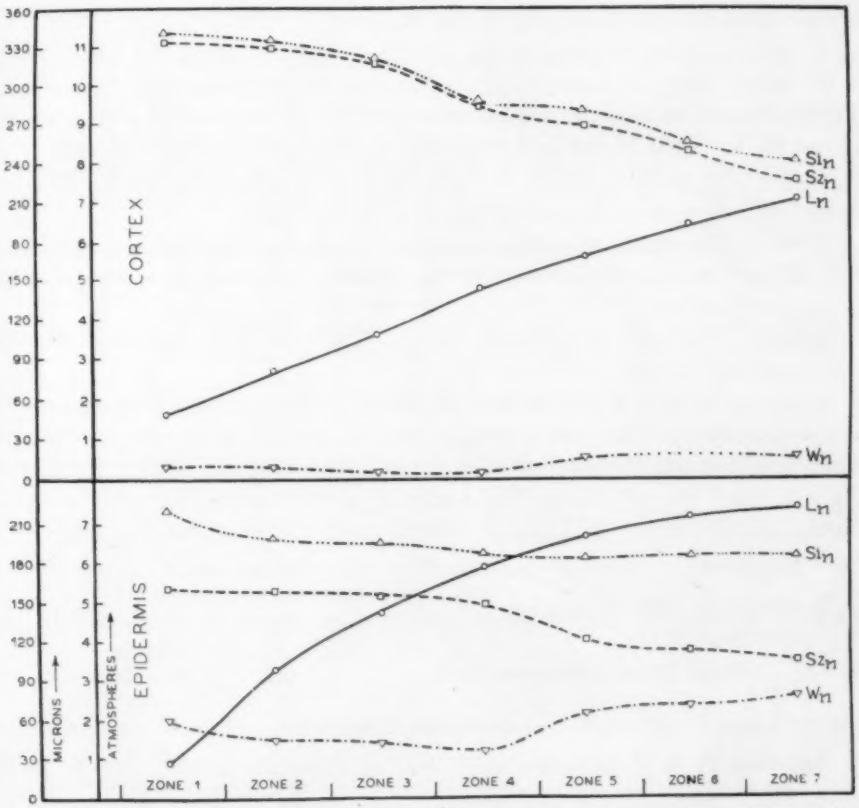

FIG. 5. Size of the cells (L_n), wall pressure (W_n), suction tension of the sap (Si_n), and suction tension of the cells (Sz_n), correlated with the age of the cells of *Helianthus* seedlings.

Zone 2. This zone contains the point of maximum rate of enlargement; it is located at 6.5 mm. from the cotyledons or 1.5 mm. from the upper limit of this zone. The cells contain a slight amount of carotinoid pigment. The viscosity of the protoplasm, the electrical charge, are less, in accord with the described gradients. The O_g, the O_n the O_s, and the Sz_n also decrease according to their respective gradients. The plasticity of the walls is still considerable, the elasticity and rigidity are negligible, the turgor is improved par-

ticularly in the lowermost part of the zone, where a bending or a stretching stress tends to break the hypocotyl less readily.

Zone 3. The protoplast and osmotic quantities change according to the described gradients. The rigidity of the cell walls is negligible, but there are indications of definite increment in rigidity which comes to clear expression in the fourth zone (see figure 4) where it manifests its influence on the wall pressure and the suction tension (see figure 5). The Sz_n potential difference is maximum for the epidermis in this zone.

Zone 4. Critical changes in the nature of the wall manifest their effects in this zone; they act disturbingly in the process of determining the osmotic quantities so that unusual care is necessary in the work. The critical point where the response to the geotropic stimulation fails to follow quickly is in this zone. The walls are no longer plastic, but are somewhat elastic. The Sz_n potential difference is maximum for the cortical tissue.

Zone 5. The elasticity of the walls decreases and the rigidity increases. The rate of increase is greater in the epidermis than it is in the cortical tissue (see figure 4).

Zone 6. The cells are almost mature. The cell walls are only slightly elastic and more rigid.

Zone 7. The cells are of maximum size, and the amount of solute present is also maximum. The wall pressure, turgor, and rigidity of the wall are maximum, but the concentration of the sap (O_n) and the suction tension of the cell (Sz_n) are minimum. The walls are hardly extensible, only slightly elastic, and the degree of rigidity is high, particularly in the epidermis (see figures 4, 5).

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BULLETIN OF THE TORREY BOTANICAL CLUB
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A NEW CONSTITUENT IN WHEAT GERM OIL

H. H. BUNZELL

In the course of our study of the vitamins present in wheat germ oil we found that wheat germ oil has a stimulating effect on the action of potato tyrosinase. This is true whether we use wheat germ oil extracted in the laboratory with ether and petroleum ether, or commercial wheat germ oil pressed (Abbott's Medicinal Wheat Germ Oil), or wheat germ oil extracted by ethylene dichloride (VioBin Corporation).

This phenomenon seems significant because of the various physiological functions with which, according to recent work, the copper enzyme, tyrosinase, seems to be concerned. Perhaps the most outstanding of these relationships is the destructive effect of tyrosinase on the vaso constrictor substance —hypertensin (8) and the oxidation of estrogens and their complete inactivation (9).

TECHNIQUE

The methods used were based on work described in earlier articles (2, 3). The simplified catox apparatus used in these experiments is shown in figure 1,[1] and has been described before (4, 7). The constant temperature chamber has also been described elsewhere (7).

The potato juice was pressed out by hand from ground peelings and was diluted with four volumes of water. In this dilution the tyrosinase activity was 0.101–0.166 Bunzell units (2, p. 40). The oxidase reagent used in this experiment was pure p-cresol. The reason for the choice of p-cresol in this connection was two-fold: one is that the mechanism of the oxidation of p-cresol by tyrosinase has been exhaustively studied by Nelson and collaborators (1). The other reason is that our work on the oxidases of potato tubers showed that p-cresol oxidation is influenced more than that of any other seventeen reagents used (5, 6).

All experiments were carried out in the presence of a phosphate buffer, pH 7. In control experiments a highly refined Russian mineral oil was used in place of wheat germ oil. In the effective experiment, dilution of the wheat germ oil when required was made with the same mineral oil.

PROCEDURE

Of the three compartments of the catox apparatus, the middle one was not used in these experiments. It served a useful purpose in assuring separation before deliberate mixing of materials placed in compartments 1 and 3. The following typical experiments will show the disposition of the materials:

[1] The plate for figure 1 was furnished by the author.

Experiment 1	Experiment 2
In compartment No. 1: 1 cc. 20% potato juice.	In compartment No. 1: 1 cc. 20% potato juice.
In compartment No. 3: 0.022 g. p-cresol, 0.5 cc. buffer sol., 0.5 cc. Rus. min. oil.	In compartment No. 3: 0.022 g. p-cresol, 0.5 cc. buffer sol., 0.0387 g. tocopherol in 0.5 cc. Rus. min. oil.

The constant temperature chamber was maintained at 35° C. The air vents (No. 7 in fig. 1) remained open until the temperature became adjusted, which required a little over a half an hour. The vents were then closed by turning the manometer (No. 5 in fig. 1) through 90° by inserting the hand through the trapdoor on top of the constant temperature box and beginning shaking, thereby mixing the components and initiating the reaction.

Rate of shaking was 140 excursions per minute; extent of excursion was 5.5 cm.

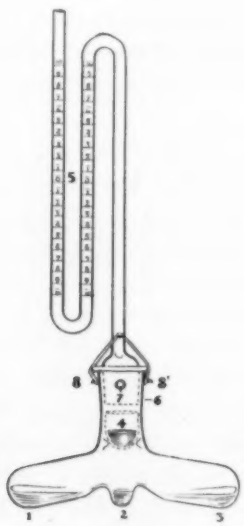

FIGURE 1

EXPERIMENTAL WORK

Readings were made as a rule at intervals of ten minutes and the experiments were of twenty-five to thirty minutes duration. For purposes of illustration a typical set of experiments is given in table 1. The data correspond to the conditions outlined under experiments 1 and 2 above.

Comparison of the final result obtained in experiment 2 with that obtained in experiment 1 shows an increase of 48%, due to the tocopherol preparation used. Throughout this paper only the last reading obtained at the end of twenty-five or thirty minutes will be used for comparison.

The selection of the proper quantity of p-cresol is important, because of its destructive effect on the tyrosinase when used above certain concentra-

TABLE 1. *The effect of tocopherol on potato tyrosinase*

Time in min.	Readings	
	Exp. 1 Control	Exp. 2 Tocopherol added
0	0.0	0.0
10	4.9	8.2
20	10.0	14.8
25	12.3	18.2

tions. For example, it was found that 0.0185 g. p-cresol used in an experiment gave a final reading of 14.0, while twice that amount, 0.0370 g., resulted in complete inhibition, presumably due to the destruction of the tyrosinase. We found it most satisfactory to use 0.022 g. p-cresol in each experiment, this being an innocuous amount and also easily measured in our calibrated micropipette.

Many experiments were performed, varying concentrations of the components of the system and also changing the physical conditions. Table 2 summarizes typical data. They are representative of all results obtained.

TABLE 2. *The effect of wheat germ oil on potato tyrosinase*

Addition	Final reading		Increase due to addition
	Control	"Addition"	
0.5 cc. wheat germ oil (made in this laboratory by extraction with ether and petroleum ether)	13.2	18.0	36.4%
0.5 cc. ditto	8.4	12.2	45.2%
0.5 cc. ditto	5.6	9.5	69.8%
0.5 cc. wheat germ oil (Abbott) pressed	13.6	18.55	36.4%
0.25 cc. ditto	12.05	16.1	33.6%
0.05 cc. ditto	13.4	17.5	30.6%
0.005 cc. ditto	11.45	13.85	21.0%
0.0005 cc. ditto	13.7	13.85	Insignificant
0.5 cc. wheat germ oil (VioBin Corporation) extracted	8.65	11.75	35.8%
0.05 cc. ditto	9.85	12.15	23.3%
0.005 cc. ditto	8.9	10.6	19.1%

All three kinds of wheat germ oil, even if used in only 1% solution (equivalent to 0.005 cc.), produced an increase in the rate of tyrosinase activity. Each set of results in table 2 represents a series of experiments carried out with fresh potato juice. There is considerable variation in the activity of the juice, since no attempt was made to use peelings of uniform thickness. This also explains why data showing an "increase" lack mathematical uniformity. Their significance is largely qualitative.

In all of the experiments here summarized, as well as all others tried, the increase in tyrosinase activity was accompanied by a difference in color. This was not observed where the difference between the control and "addition" experiments was insignificant (table 2, line 8). The reaction mixture of the control experiments was dark brown; that of the addition experiments, brick red. The dark red color could be extracted with methyl alcohol, indicating the presence of OH groups. Ether or chloroform extracts were colorless. The brick red color in the "addition" experiments was not soluble in alcohol, but gave a bright yellow solution with ether or chloroform. The bright yellow color of the extracts would indicate the presence of quinoid groups. There is every indication that in the stimulation experiments, there is not only a speeding up of the reaction, but also the formation of a different oxidation product.

Wheat germ oil contains, besides the vitamins of the E complex, vitamin A. To determine whether the vitamin A content of the wheat germ oil is related to the effect here described, we evaluated the vitamin A content of the VioBin wheat germ oil in terms of White's vitamin A preparation. The latter contained 108,100 U.S.P. units per gram. The comparison was made in a "Lumetron" electrical colorimeter using isopropyl alcohol as a solvent. It was found that a 10% solution of VioBin oil would contain per gram the equivalent of 0.00195 g. of the vitamin A oil used for comparison. This corresponds to a 0.2% solution of the comparison preparation. Table 3 shows results obtained at the end of thirty minutes. Experiments 1 and 3 are controls containing 0.022 g. p-cresol, 0.5 cc. water, 1 cc. 20% potato juice, and 0.5 cc. cotton seed oil. Experiments 2 and 4 contained the same reagents, except that the cotton seed oil was replaced by an equal amount of a 0.2% solution of vitamin A oil (White) in cotton seed oil. The amount of vitamin A in experiments 2 and 4 would equal that contained in the same volume of 10% VioBin wheat germ oil solution in cotton seed oil.

TABLE 3. *The effect of vitamin A on potato tyrosinase*

Experiment	1	2	3	4
Final reading	12.4	12.0	12.5	11.8

Comparing the average of 1 and 3, i.e., 12.45, with the average of 2 and 4, i.e., 11.9, we find that no increase is brought about by the vitamin A. This result is corroborated by the lack of any difference in coloration in the ultimate mixtures.

The next most obvious thought is that α tocopherol might be responsible for the effect. We secured a pure *d,l* α tocopherol from Merck and Company.

The material was weighed directly into the catox apparatus. Results are shown in table 4.

TABLE 4. *The effect of d,l α tocopherol on potato tyrosinase*

In each trial the following substances were used: 0.022 g. p-cresol, 0.5 cc. buffer, 1 cc. 20% potato juice, and Russian mineral oil and *d,l* α tocopherol as indicated below.

Experiment	1	2	3
	Control 0.5 cc. Rus. min. oil	0.0045 g. *d,l* α tocopherol in 0.5 cc. Rus. min. oil	0.0071 g. *d,l* α tocopherol in 0.5 cc. Rus. min. oil
Final reading	14.95	14.8	14.7
Experiment	4	5	6
	Control 0.5 cc. Rus. min. oil	0.0114 g. *d,l* α tocopherol in 0.5 cc. Rus. min. oil	0.0195 g. *d,l* α tocopherol in 0.5 cc. Rus. min. oil
Final reading	14.2	14.3	13.8

Results given in table 4 show that *d.l* α tocopherol (Merck) does not stimulate the action of tyrosinase. These results are corroborated by the fact that in both sets there was no difference in the color of the final reaction mixtures when the controls were compared with the corresponding tocopherol experiments. The color in all cases was dark brown.

We next tried a preparation of α, β, and γ tocopherol (Abbott Laboratories). This is made by the distillation of certain vegetable oils and contains 25% of a mixture of the three tocopherols. We have been unable to learn anything about the nature of the vegetable oils used besides wheat germ oil, nor have we been able to establish the relative amounts of α, β, and γ tocopherol in the mixture. Results are given in table 5.

TABLE 5. *The effect of α, β, γ tocopherol on potato tyrosinase*

In each trial the following substances were used: 0.022 g. p-cresol, 0.5 cc. buffer, 1 cc. 20% potato juice, and Russian mineral oil and α, β, γ tocopherol as indicated below.

Experiment	1	2	3
	Control 0.5 cc. Rus. min. oil	0.0335 g. α, β, γ tocopherol in 0.5 cc. Rus. min. oil	0.0387 g. α, β, γ tocopherol in 0.5 cc. Rus. min. oil
Final reading	12.3	16.7	18.2

The α, β, γ tocopherol preparation furnished by Abbott produced a pronounced increase in the tyrosinase activity. In experiment 2 (table 5) the increase was 25%, in experiment 3, 47.9%; the color in the control was the usual dark brown, while in the tocopherol experiments the color of the final reaction mixtures was brick red.

CONCLUSIONS

There is in wheat germ oil a constituent which speeds up the tyrosinase oxidation of p-cresol. This effect is not produced by the vitamin A in the oil or by the alpha tocopherol. It may be produced by beta or gamma tocopherol or by some other constituent of wheat germ oil. Owing to the extremely small concentration of vitamin K in wheat germ we are not inclined to attribute the effect to K. This point however, is being investigated in this laboratory.

Under the influence of the substance studied a different oxidation product is formed. This appears to be of quinoid character. It is possible that, in normal tyrosinase oxidation of p-cresol, the unstable hydroxyquinone formed as the third stage of the oxidation spontaneously disappears, while in the presence of the new component, it combines with it and thus becomes stabilized (10, pp. 198, 199).

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CROSSING-OVER AND SECOND DIVISION SEGREGATION IN FUNGI

FRANCIS J. RYAN

In some fungi the segregation of genetic factors can be determined by the linear order in which different phenotypes are distributed among the "sexual" spores. When two mutant characters are found in the order A A a a the best interpretation is that the alleles responsible for them have separated in the first meiotic division. On the other hand when the arrangement is A a A a or A a a A they have separated in the second division (Dodge 1927; Wilcox 1928). Such second division segregations have been explained by many mycologists in terms of a disjunction of homologous chromosomes during the second meiotic division. Dodge (1940) has shown, however, that in many cases there is an equally possible alternative explanation which involves the more modern but now classical notions of first division disjunction and crossing-over. Despite Dodge's suggestion, there are two studies on inheritance in ascomycetes which apparently confirm with genetic data the old mycological point of view. Both Wülker (1935) and Zickler (1934), who are aware of the view now prevalent among geneticists that alleles may be reduced (separated) in either the first or second meiotic division, contend that second division disjunction of homologous spindle fiber attachments or kinetochores (centromeres) must also be invoked to explain their experiments with *Neurospora* and *Bombardia* respectively. This of course implies that each kinetochore is divided in the first division, an unprecedented happening in the normal meiosis of other organisms. To date no adequate refutation based upon an analysis of their extensive data has been made.

Zickler was fortunate in being able to determine certain genotypes among his ascospores without dissection and germination because some of the genes with which he dealt affected the color of the ascospores themselves as well as the mycelia they produced. In a cross of the *viridis* and *lactea* mutants the arrangement of greenish and colorless spores in the intact ascus showed that second division segregation took place in 66.4 per cent of 2355 asci. This, Zickler pointed out, would occur if the separation of the four chromatids into pairs in the first meiotic division occurred at random. That is, each chromatid has an equal chance to associate with each of three others. Since only one of the others is a sister chromatid while two are non-sisters, first division segregation (association of sister chromatids) occurs half as frequently as second division segregation (association of non-sister chromatids).[1]

[1] Wülker believes the ratio would be 1: 1 instead of 2: 1 if the separation into pairs were random. His error lies in the fact that he considered only separations along the equa-

If Zickler's interpretation is correct then *all* factors, irrespective of their location on the chromosome, should show second division segregation in two thirds of the cases.

In a cross of *viridis* and *rubiginosa* mutants, however, 8204 asci containing greenish and reddish spores showed 64 per cent second division segregation. Zickler himself calculated that this percentage was significantly different from 66.7 per cent by statistical test. In an attempt to explain this discrepancy he concluded that something (external) must have influenced the random separation of the individual chromosomes or suppressed their longitudinal split.

Zickler may be correct in assuming that some uncontrolled (although perhaps genetic) variable is influencing the number of second division segregations. For *viridis*, *rubiginosa* and *lactea* are multiple alleles and, although he does not believe so, they would be expected to show the same percentage second division segregation. Nevertheless, the task at hand is to determine whether a second division disjunction is the necessary interpretation of these data.

The problem can be approached by an analysis similar to that which Lindegren (1933) used in his studies on *Neurospora*. Since color is linked with sex in *Bombardia* the percentage of new combinations of the two factors can be calculated and compared with the sum of one half of the percentages of second division segregation of these factors. (The percentages are halved in order to obtain values comparable to those secured in *Drosophila* where only one half of all cases of crossing-over are observed since only one of the four chromatids is recovered.) In the case of a first division disjunction with a single crossing-over these values are equal. For example, if we assume crossing-over to occur in all asci as outlined in figure 1, the genotypes recovered in the haploid spores would be AB, aB, Ab, and ab. Thus, there are 50 per cent new combinations. Second division segregation of A from a (A a A a) would occur in 100 per cent of the cases and this divided in half is 50. Here segregation of B from b in the second division (B b B b) never occurs and so the final value based on second division segregation is 50. This is exactly the same as that calculated on the basis of new combinations. When we assume crossing-over to occur only in some cases the values are smaller but still remain equal—each crossing-over results in a second division segregation so that two of four chromatids have new combinations of genes. From an agreement of this sort in *Neurospora*, Lindegren correctly concluded not only that there was crossing-over in the four strand stage but that homologous kinetochores separated in the first division.

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tional or reductional splits and failed to consider diagonal aggregations across both of these planes.

On the other hand, if it were granted that there is a random assortment of the four chromatids during meiosis as well as crossing-over, an hypothesis which Ziekler considered, then the above comparison yields very different results (fig. 2). Here the genotypes recovered and their order would be:

AB	aB	Ab	ab	= 33.3%
AB	ab	aB	Ab	= 33.3%
AB	Ab	aB	ab	= 33.3%
				100.0%

50 per cent of these are new combinations. However, since there is 66.7 per cent second division segregation of both A and B a value of 66.7 is obtained which is quite different from the value based on new combinations. If one

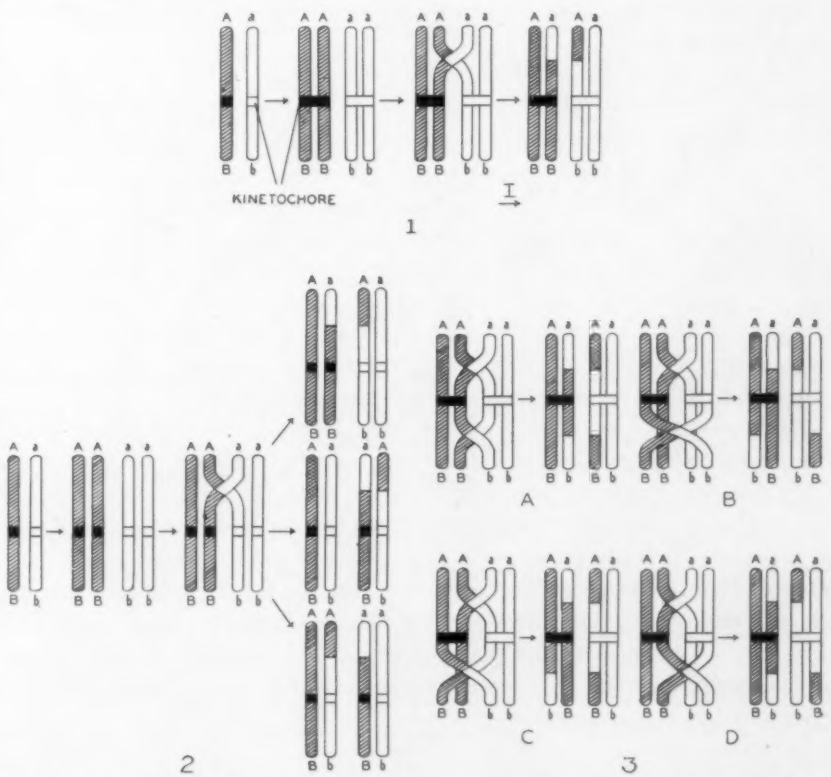

FIG. 1. Orthodox behavior of chromatids during the first meiotic division involving crossing-over and first division disjunction of homologous kinetochores (I). The kinetochores split in the second division. FIG. 2. Hypothetical behavior of chromatids during the first meiotic division assuming crossing-over and random segregation of kinetochores which split in the first division. FIG. 3. Double crossing-over with first division disjunction of homologous kinetochores which results in *old* and new combinations and second division segregation of genetic factors.

assumes that the attraction of *sister chromatids* is somewhat greater than that between non-sisters then there is a closer correspondence of values calculated by the two methods. The values eventually coincide when sister attraction is complete but this situation is identical with first division disjunction of kinetochores discussed in the paragraph above.

If we assume crossing-over to occur only in some cases the value of 66.7 is still obtained from second division segregations just as it was when we assumed either that there was no crossing-over or that crossing-over occurred in all of the cases. However, the value obtained from new combinations decreases in proportion to the decrease in percentage of crossing-over and in this way the discrepancy between the two values increases.

Thus a method seems available for determining whether a second division segregation is the result of a first or a second division disjunction of homologous kinetochores.

The only evidence which Zickler gives that could be put to this test is in a footnote. Here he states that there were only 37.1 per cent new combinations of color and sex in the *rubiginosa-viridis* cross. Zickler found 57.7 per cent[2] second division segregation of color and 62.7 per cent second division segregation of sex. These divided in half are arbitrary measures of the map distance of the loci from the kinetochores. Therefore 28.9 and 31.4 may be either added or subtracted according to whether the color and sex loci are on the same or opposite sides of the kinetochore. Since neither of the resultant values of 60.2 or 2.5 correspond with the map distance calculated from new combinations, Zickler concludes that crossing-over cannot explain the frequency of first and second division segregations.

Stripped to its essence, however, this lack of correspondence simply means either that all the second division segregations of *rubiginosa* from *viridis* did not result in new combinations with sex (60.2 compared with 37.1) or that all the new combinations were not the result of second division segregations (37.1 compared with 2.5). This is exactly what could be expected if double crossovers had occurred (fig. 3). Such crossovers can yield both new and *old* combinations and yet the result is always second division segregation. If we assume for the time being that the four possible types of double crossing-over occur in equal proportions then the following genotypes are obtained in the order shown:

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[2] Zickler consistently found a smaller percentage of second division segregations of *viridis* from *rubiginosa* when he dissected and germinated ascospores than he found by direct count in the asceus. For example, in this experiment he found 57.7 per cent compared with 64.0 per cent—an even greater deviation from the 66.7 per cent predicted on the basis of random segregation of kinetochores. The discrepancy between results obtained by different types of analyses he likewise attributes to environmental influence.

AB	ab	AB	ab	= 25%
Ab	aB	Ab	aB	= 25%
Ab	aB	AB	ab	= 25%
AB	ab	Ab	aB	= 25%
				100%

There are 50 per cent new combinations. But there are 100 per cent second division segregations of both A and B so that a value of 100 is obtained to compare with 50. It is obvious there is a discrepancy resembling that between the values of 37.1 from recombinations and 60.2 from second division segregations obtained in the *viridis-rubiginosa* cross. (The value 2.5 will not be considered because it may not be significantly different from 0 and at any rate it is not predicted by the hypothesis of random segregation of homologous kinetochores.)

The discrepancy between the values for second division segregation and new combinations can be corrected by the use of the equation $m + n - 2\,mn = \%$ new combinations between color and sex (Haldane 1919) where m = map distance or recombination between color and kinetochore and n = map distance or recombination between sex and kinetochore. This is simply a subtraction of an estimate of the percentage of old combinations formed by double crossing-over which give rise to second division segregation (see figure 3) from the percentage of new combinations expected if there were no double crossing-over. Solving, $.289 + .314 - .181 = .422$, or 42.2 per cent new combinations are expected from the data on second division segregation when double crossing-over is taken into account and, as was assumed, crossing-over is random. This is rather close correspondence with the observed value of 37.1 per cent. The small difference between the two may be due to the presence of more double crossing-over than would be expected on the basis of chance. This would increase the value of mn in the equation and decrease the percentage of new combinations expected. Such an explanation seems reasonable in view of the fact that non-random crossing-over appears to occur among molds (Lindegren and Lindegren 1937, 1939; Whitehouse 1942).

It would be possible to determine decisively whether Zickler's ratios were the result of double crossing-over, were it possible to analyze the genotypes and orders of spores from the *viridis* × *rubiginosa* cross. Unfortunately, Zickler does not present his original data so that this point cannot be finally decided.

Wülker fortunately does present his original data on *Neurospora* and so it is possible to determine directly the proportion of ascus arrangements resulting from double crossing-over. Indeed, recognizing this possible interpretation, he carried out the analysis himself and showed how all the arrangements he found could be explained in terms of crossing-over. But

the presence of 28 asci resulting from three-strand crossing-over (fig. 3, C and D) compared with 8 asci resulting from two-strand crossing-over (fig. 3, A) and 8 resulting from four-strand crossing-over (fig. 3, B) seemed disproportionate to him. Consequently he made an elaborate estimate of the proper ratios of first and second division disjunctions combined with several types of crossing-over which would yield the ascus types he observed. It is not necessary to discuss these estimates because Wülker revealed the critical point for his hypotheses in these words which are freely translated—"The appreciation of all following calculations depends *alone* upon recognizing in the value of 28 asci a deviation from the numbers expected exclusively from crossing-over which cannot be explained in other ways." Accordingly, if it is possible to show that 28 asci resulting from three-strand crossing-over is not beyond expectation in Wülker's results, it is not necessary to accept his scheme for second division disjunction.

In the first place the total number of double crossovers across the kinetochore (it is impossible to calculate the expected percentage of crossing-over in one arm because only one gene was studied in each arm), 24.4 per cent, resembles that calculated from the frequency of single crossing-over, 24.8 per cent. Moreover, it can be seen from figure 3 that the expected ratio of two-, three- and four-strand double crossing-over occurring at random is 1:2:1. When a χ^2 test is applied to the fit of the 8 two-strand, the 28 three-strand, and the 8 four-strand double crossover asci to the 1:2:1 ratio a P of 0.2 is obtained indicating a good fit to the crossing-over hypothesis for such a small number of cases,[3] thus:

Number of strands involved in double crossing-over	2	3	4
Actual number of asci	8	28	8
Expectation (e)	11	22	11
Deviation (d)	3	6	3
d^2	9	36	9
$\frac{d^2}{e}$	0.82	1.64	0.82

$$\Sigma\frac{d^2}{e} = \chi^2 = 3.28 \qquad P = 0.2$$

We may conclude therefore that in *Neurospora* the genetic evidence indicates first division disjunction of kinetochores and crossing-over.

In summary, it is certain that Zickler's data on *Bombardia*, as presented, are not crucial in demonstrating either a first or a second division disjunction of homologous kinetochores. The crucial data for establishing first division disjunction—the recognition of double crossing-over—may be in his original records but are not presented in his report. Neither has he found the data crucial for a demonstration of a second division disjunction—

[3] It is interesting to note that Wülker's data on *Neurospora sitophila* provide no evidence for the non-random crossing-over found by Lindegren for *N. crassa*.

namely, that all factors irrespective of their location on the chromosome show second division segregation in two-thirds of the cases. In short, if single and double crossing-over occurs, as seems likely, the data can be explained on an orthodox genetic basis. Moreover, besides Wülker's demonstration that the ascus types he obtained in *Neurospora* can be explained in terms of first division disjunction and crossing-over, it is possible to show that even the ratios of these types to one another are as would be expected on this basis. This is critical evidence on behalf of first division disjunction of kinetochores.

Thus, there is every reason to believe that, in molds as in other organisms, homologous kinetochores separate in the first meiotic division (reductionally) and each kinetochore divides in the second division (equationally).

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THE NUMBER OF CHROMOSOMES IN TWO SPECIES OF AMORPHOPHALLUS

CLYDE CHANDLER

Plants of the genus *Amorphophallus* are native of the tropics. The giant forms of this genus are quite often grown as curiosities in hot houses in the more temperate regions. The size and structure of the inflorescence, the flower behavior, the short period of bloom, and the infrequency of bloom on these plants in cultivation create interest for both the casual observer and the scientist.

Few cytological observations have been reported for this entire genus of approximately 90 species. Stout (1937) reported observations on the pollen, the result of germination tests and the relation of the pollen tubes to the style for one plant of *A. titanum*. The writer knows of no report concerning the number of chromosomes in any plant of this genus.

Plants of two species of *Amorphophallus* have flowered in the conservatories of The New York Botanical Garden. A sixty-pound corm of *A. titanum* which was obtained by Dr. E. D. Merrill (1932) from A. M. Oostingh, Fort de Kock, Sumatra, in June, 1932, flowered in June 1937. An accurate description of the flowering of this corm was published in the Journal of The New York Botanical Garden (August 1937). Root tips were collected from the corm when it was removed from its tub three days after flowering. These root tips were not actively growing and none had mitotic figures.

Another smaller corm of *Amorphophallus titanum* was collected in Sumatra by Mr. B. A. Krukoff and sent to the Garden in 1935 (accession no. 77023). When the plant which was obtained from this corm was actively growing, root tips were collected and fixed for cytological observations. Later when the plant flowered in July 1939 it was identified as *A. titanum*. It was somewhat smaller than the plant which flowered in 1937.

The root tips were fixed in Flemming's medium fixative, sectioned, and stained with Heidenhain's hematoxylin. Each of the seventeen somatic cells in which the entire complement of chromosomes could be counted contained 26 chromosomes. A study of these showed that there were present 13 pairs of homologous chromosomes. It appears then that there were two sets of 13 chromosomes each. The members of one of these sets are shown in figure 1.

As shown, there were distinct differences in the size and shape of the chromosomes in each set. The longest chromosomes were about three times the length of the smaller ones. Since it was not convenient to make smear preparations of pollen-mother-cells the exact location of the spindle fiber

insertion regions was not determined. It seemed, however, that two of the chromosomes had median, four had submedian, and seven had terminal or sub-terminal insertion regions.

Plants of *Amorphophallus bulbifer* have been growing in the New York Botanical Garden greenhouses since 1902 when several corms were received from Edinburgh (accession no. 14468). Cytological studies of the root tips of a plant of *A. bulbifer* revealed that it had 36 chromosomes in its somatic cells. Study of these chromosomes seemed to indicate that each of the two sets of homologs was composed of 18 chromosomes which were somewhat morphologically different from one another. One set of 18 chromosomes is shown in figure 2. Only three chromosomes here designated B, O, and K, of *A. bulbifer*

1

2

FIG. 1. One set of chromosomes in the somatic tissue of *Amorphophallus titanum*.
FIG. 2. One set of chromosomes in the somatic tissue of *Amorphophallus bulbifer*.

appeared to be closely similar to chromosomes A, D, and K of *A. titanum*. All other chromosomes in a single set differed from one another as well as from all other chromosomes of *A. titanum*. Five of these chromosomes seemed to have median insertion regions, nine had sub-median and four had terminal or sub-terminal spindle fiber insertion areas.

Gaiser (1930) lists the number of chromosomes for 57 species of plants of the family Araceae. It is to be noted that *Arisaema serratum* var. *Thunbergii* f. *Blumei* is the only species for which the diploid number of 26 chromosomes is given. No species is accredited with 36 chromosomes in the somatic tissue. However, the 2n number of chromosomes in *Anthurium crassinervium* and *A. Wallisii* is ca. 60 and *A. radicans* is given as 50. The haploid number of 15 seems most frequent while 8, 9, 10, 12 and 16 have been observed in various species of the Araceae.

In this study it has been determined that for the plants studied the diploid number of chromosomes in somatic cells of *Amorphophallus titanum* is 26 and that for *A. bulbifer* is 36. Assuming that these are all in homologous pairs the haploid numbers for these plants are 13 and 18. And it is the giant species which has the lower number. These numbers do not indicate a simple polyploid relationship for these two species.

There is, however, a striking resemblance between chromosomes A and B; C and D; H, I, J and K; and M and N of a single set from *A. bulbifer* as may be observed in figure 2.

THE NEW YORK BOTANICAL GARDEN
NEW YORK

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THE GENUS STACHYURUS

HUI-LIN LI

In this study an attempt is made to summarize our present knowledge of the taxonomy of the genus *Stachyurus*, on the basis of the material available in the herbarium of the Arnold Arboretum of Harvard University. So complete is this material that only one recently described Japanese species, *S. ovalifolius* Nakai, has not been seen by this writer represented either by a type or a classical specimen. The types of the few varieties described in this paper are deposited in the herbarium of Arnold Arboretum.

Stachyurus was first described by Siebold and Zuccarini for *S. praecox*, a Japanese species, and included in the Pittosporaceae (Sieb. & Zucc. Fl. Jap. **1**: 43. 1835). Bentham (Jour. Linn. Soc. **5**: 55. 1861; Benth. & Hook. Gen. **1**: 184. 1862) later transfers it to the Ternstroemiaceae. To both of these families the genus is only remotely related. Gilg (in Engl. & Prantl, Nat. Pfl. **3** (6): 192. 1893) more appropriately creates for it the family Stachyuraceae and gives it a detailed treatment. Only two species were known at that time, namely, *S. praecox* Sieb. & Zucc. of Japan and *S. himalaicus* Hook. f. & Thomson of the Himalayan region. In the second edition of the Natürlichen Pflanzenfamilien (1925), the same treatment is reprinted without any additional data.

The forms treated in this review are all that are known at present, totaling twelve species and four varieties. The leaves are of special use in making taxonomic determinations. The shape, size, apex, base, margin, and venation of the leaves, as well as the length of the petioles, are used extensively to distinguish the different species. The length of the inflorescences, pedicels, and styles is also useful in identification. The flowering parts, except for minor points pertaining to the length of the styles, exhibit little variation. The size and shape of the fruit are sometimes essential for species identification.

Franchet (Jour. de Bot. **12**: 254. 1898) divides the genus into two sections, *Callosurus* and *Gymnosurus*. He characterizes the two sections as follows: "Sectio 1. Callosurus.—folia racemos axillentia persistentis; racemi pedunculati. Sectio 2. Gymnosurus.—folia racemos axillentia ante anthesim decidua; racemi sessiles." To the first section belong *S. yunnanensis* Franch. and *S. obovatus* (Rehder) Li, and to the second section the remaining species. The peduncles in the first section are rather short and not always distinct, but in the second section the inflorescences are invariably sessile or subsessile.

The inflorescences in both sections are spikes or racemes arising from the axils of leaves, usually produced by one-year-old wood. The differences that

Franchet emphasizes in his diagnostic summary are best interpreted as follows:

Sect. *Callosurus:* The spike grows on a normal axillary florescent axis, that is, without tending to displace or to suppress the leaf itself, and the leaf consequently persists throughout the flower- and fruit-stage.

Sect. *Gymnosurus:* The spike tends to eliminate the leaf, which is caducous; the result is that the inflorescences and infructescences are borne without a subtending leaf.

The basis of this difference, which Franchet fails to notice, is essentially physiological, and presumably, to a certain extent, also anatomical. In *Callosurus,* the part of the stem that bears the flowers and fruits remain essentially a vegetative axis with lateral inflorescences. In *Gymnosurus,* on the contrary, the same part of the stem tends to become a floriferous axis, in a manner suggestive of an apical or intercalary inflorescence. The passage from one form of habit to the other is subtle and may, in certain species, be apparent only as a tendency, but it is marked enough to justify the retention of Franchet's sections and characterizations.

Stachyurus is confined to the temperate regions of eastern Asia, extending from the eastern Himalayas in the west to the Bonin Islands in the east, but not ranging below 20° N. Lat. It is known in northern Burma, Tonkin, and Kwangtung proper, but apparently it is lacking in Hainan Island. On the Asiatic mainland, the spread of the genus scarcely extends northward to 35° N. Lat., but it is found in all parts of the Japanese Archipelago as far north as Hokkaido. The species are local in their distribution, except *S. praecox* Sieb. & Zucc., which is widely distributed in Japan proper, *S. chinensis* Franch. and its varieties, which are known in all the Chinese provinces where the genus is recorded, and *S. himalaicus* Hook. f. & Thomson, which extends from eastern India through southern China to Formosa.

STACHYURUS Sieb. & Zucc. Fl. Jap. **1**: 42. *pl. 18.* 1835; Endl. Gen. Pl. **2**: 1083 (n. 5669). 1840; Benth. & Hook. Gen. **1**: 194. 1862; Gilg in Engl. & Prantl, Nat. Pfl. **3** (6): 193. 1893; ed. 2. **21**: 458. 1925; Rehder, Man. Cult. Trees & Shrubs 640. 1927; ed. 2. 654. 1940.

Shrubs or small trees, deciduous or evergreen, glabrous, often with straggling branches, the branchlets with large pith, the winterbuds small, with 2–4 outer scales; leaves alternate, the petioles slender, the blades membranaceous to coriaceous, serrulate; stipules small, caducous; flowers small, regular, perfect or functionally dioecious, sessile to short-pedicellate, in erect or pendulous racemes or in spikes axillary on last years branches, with one bract at the base of the pedicel and two bracteoles subtending the flower; sepals and petals each four, free, imbricate; stamens 8, distinct, the anthers versatile; ovary superior, incompletely 4-celled by the intrusion of the parietal placentae, the style simple, short, the stigmas capitate, 4-lobed, the ovules many; fruit berry-like, with leathery pericarp; seeds many, small,

with soft arillus, albuminous, the embryo straight, the cotyledons elliptic, the radicles short.

TYPE SPECIES: *Stachyurus praecox* Sieb. & Zucc.

KEY TO THE SPECIES AND VARIETIES

A. Leaves at the base of the inflorescence persistent; inflorescences short-pedunculate. (Section I. *Callosurus* Franch.)
  B. Leaves ovate to oblong-ovate; inflorescences 3–9 cm. long, with 12–22 flowers or fruits.
    C. Fruits subsessile or very short-pedicellate, the pedicels to 1 mm. long ..... 1. *S. yunnanensis.*
    CC. Fruits long-pedicellate, the pedicels 3–5 mm. long, articulate at the middle ..... 1a. *S. yunnanensis* var. *pedicellatus.*
  BB. Leaves obovate to oblong-obovate; inflorescences about 1.5 cm. long, with 3–8 (rarely 10) flowers or fruits ..... 2. *S. obovatus.*
AA. Leaves at the base of the inflorescence early deciduous; inflorescences sessile or subsessile. (Section II. *Gymnosurus* Franch.)
  B. Leaves oblong-lanceolate to linear-lanceolate, about 3 times or more as long as broad, the marginal teeth very fine, mostly close.
    C. Leaves with longitudinal veins located a little more than half way between the midrib and margin, united with the straight or slightly curved lateral nerves.
      D. Leaves narrowly linear-lanceolate, the base acute, the serrations more or less remote, inconspicuous, incurved and obtuse ... 3. *S. salicifolius.*
      DD. Leaves oblong-lanceolate, the base cordate, the serrations fine, very close, more or less straight and pointed, rigid ..... 4. *S. cordatulus.*
    CC. Leaves without longitudinal veins, the lateral nerves ascending and prolonged.
      D. Leaf-base acute, the apex acuminate, the marginal teeth sharp-pointed; petioles about 2.5 cm. long; inflorescences about 10 cm. long ..... 5. *S. himalaicus.*
      DD. Leaf-base cordate, the apex long-acuminate, the marginal teeth slightly incurved and obtuse; petioles about 4.5 cm. long; inflorescences about 14 cm. long ..... 6. *S. lancifolius.*
  BB. Leaves ovate-oblong to orbicular, about 2 times or less as long as broad, the marginal teeth coarse, generally more remote.
    C. Leaves ovate-oblong, about 2 times as long as broad (Japanese species).
      D. Leaves long-petiolate, the petioles 3–5 cm. long; fruits large, 1.3–2 cm. long.
        E. Leaves long-acuminate, the base rounded to subcordate, the marginal teeth prominent, pointed; inflorescences robust, about 8–9 cm. long; fruits oblong-obovate, 1.3–5 cm. long ..... 7. *S. Matsuzakii.*
        EE. Leaves acute, the base broadly acute, the marginal teeth less prominent, obtuse; inflorescences slender, 4–5 cm. long; fruits broadly oblong, 1.8–2 cm. long.
          F. Lateral nerves about 6 on each side ..... 8. *S. macrocarpus.*
          FF. Lateral nerves 9–11 on each side. 8a. *S. macrocarpus* var. *prunifolius.*
      DD. Leaves with petioles about 1.5–2 cm. long; fruits small, about 1 cm. long ..... 9. *S. praecox.*
    CC. Leaves ovate to orbicular, as long as to less than 2 times as long as broad (Chinese species).
      D. Leaves acuminate or cuspidate.

E. Leaves ovate, the apex long-acuminate, the base acute to rounded ..... 10. *S. chinensis.*
EE. Leaves orbicular, the apex abruptly short-acuminate or cuspidate, the base cordate.
F. Leaves abruptly acuminate, the acumen 5–8 mm. long. 10a. *S. chinensis* var. *latus.*
FF. Leaves cuspidate-emarginate, the acumen 10–15 mm. long ..... 10b. *S. chinensis* var. *cuspidatus.*
DD. Leaves emarginate or bilobed ..... 11. *S. retusus.*
No specimen observed ..... 12. *S. ovalifolius.*

1. STACHYURUS YUNNANENSIS Franch. Jour. de Bot. **12**: 253. 1898; Rehder in Sarg. Pl. Wils. **1**: 288. 1912; Jour. Arnold Arb. **15**: 103. 1934; Chung, Mem. Sci. Soc. China **1**: 176. 1924; Hand.-Maz. Symb. Sin. **7**: 383. 1931. *Stachyurus Esquirolii* H. Lévl. Fl. Kouy-Tchéou 416. 1915. Figure 1.

A shrub, 1.5–3 m. tall, the branchlets olivaceous, with lenticels; leaves coriaceous, persistent, glabrous, greenish and slightly lustrous above, pale beneath, ovate-oblong to ovate-lanceolate, 6–12 cm. long, 2–4 cm. wide, the apex caudate-acuminate, the base acute, the margins finely and sharply serrulate, the teeth pointed, with callose apices, the lateral nerves 5–7 on each side, ascending, inconspicuous to subconspicuous above, slightly elevated and conspicuous beneath, the tertiary veins inconspicuous on both surfaces; petioles 1–2.5 cm. long; inflorescences 6–10 cm. long, erect or pendulous, short-pedunculate, the peduncles 0.5–1 cm. long, the flowers yellow, subsessile, the bracts triangular-ovate, acuminate, about 2.5 mm. long, the bracteoles ovate, acute, about 3 mm. long; sepals ovate, about 4.5 mm. long, acute; petals obovate, obtuse, 6–7 mm. long, about 4 mm. wide; filaments about 5 mm. long; ovary and style about 6 mm. long, scarcely exerted, the stigmas capitate, distinct; fruit globose, about 6 mm. across, sessile, with persistent style.

CHINA: SZECHUAN: Hung-yah Hsien, *E. H. Wilson 2555;* Ping-pien Hsien, *H. T. Tsai 62960;* Mt. Omei, *W. P. Fang 2634, T. T. Yü 399, 405, Y. S. Liu 1623, 1668, 1776, C. Y. Chiao & C. S. Fan 71, 235, K. N. Yin 138.* YUNNAN: Mo-so-yn (Lou Kong), *Delavay 822* (syntype, photo. and merotype of leaf in AA), April, 1884, *3334* (syntype, merotype of flowers in AA); Champutong, Der-la, *C. W. Wang 66805.* KWEICHOW: Than-lo, *J. Esquirol 3517* (holotype of *S. Esquirolii* H. Lévl., merotype in AA); An-lung, Kow-chang, *Y. Tsiang 7418;* Kweiyang, Chan Lin Shan, *S. W. Teng 90021.*

This species can be distinguished from the other two common Chinese species of the genus, *S. himalaicus* Hook. f. & Thomson and *S. chinensis* Franch., by the fact that the leaves at the base of the racemes are persistent rather than early deciduous. The leaves of *S. yunnanensis* resemble those of *S. himalaicus*, differing, in addition to the character mentioned above, in the generally smaller size and coarser and more remote serrations.

1a. STACHYURUS YUNNANENSIS Franch. var. PEDICELLATUS Rehder in Sarg. Pl. Wils. **1**: 288. 1912; Chung, Mem. Sci. Soc. China **1**: 176. 1924. Figure 2.

Differs from the species in the distinctly pedicellate fruit, the pedicels 3–5 mm. long, articulate at the middle.

CHINA: SZECHUAN: Yung-yang Hsien, *E. H Wilson 4541* (holotype) July, 1910. YUNNAN: Loping, Tjitjischan, *H. Handel-Mazzetti 27 = 10188* (immature fruits; identified by Handel-Mazzetti as *S. yunnanensis* Franch.).

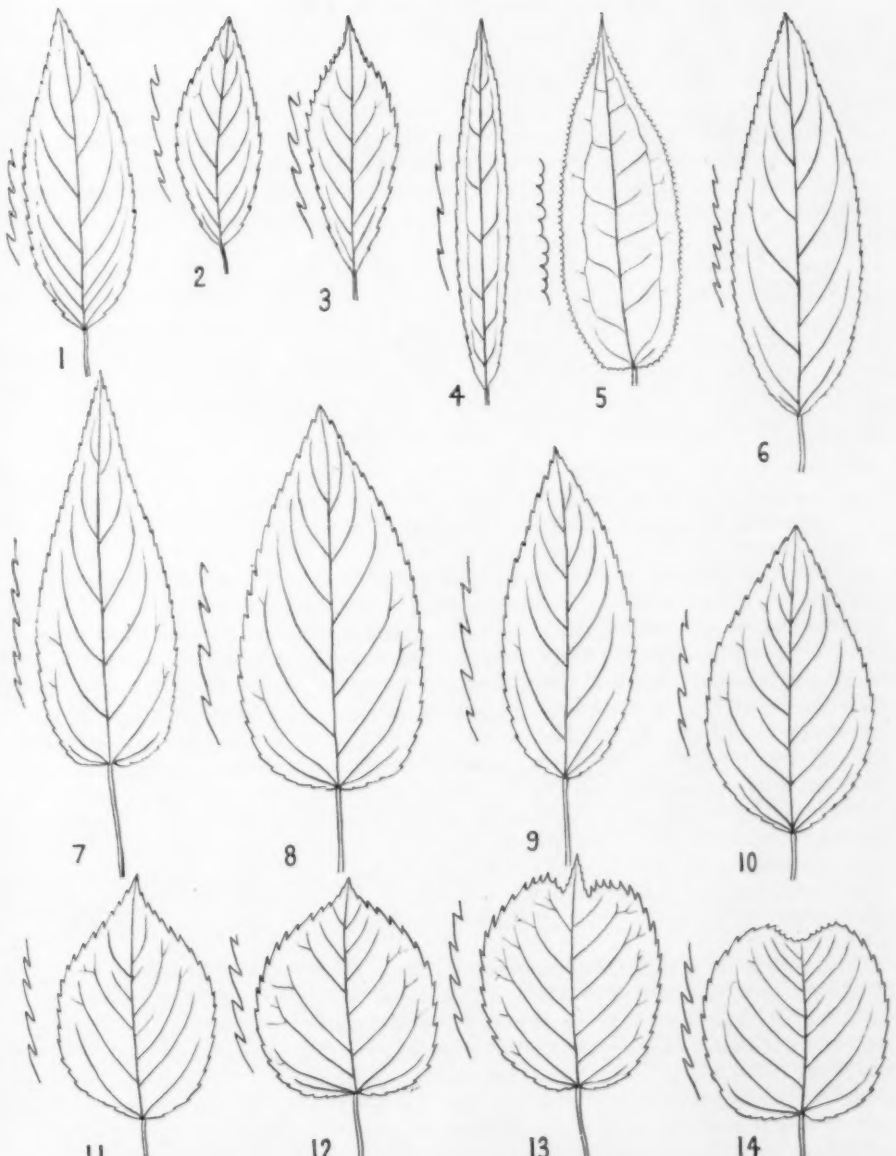

FIG. 1. *Stachyurus yunnanensis*. FIG. 2. *S. yunnanensis* var. *pedicellatus*. FIG. 3. *S. obovatus*. FIG. 4. *S. salicifolius*. FIG. 5. *S. cordatulus*. FIG. 6. *S. himalaicus*. FIG. 7. *S. lancifolius*. FIG. 8. *S. Matsuzakii*. FIG. 9. *S. macrocarpus*. FIG. 10. *S. praecox*. FIG. 11. *S. chinensis*. FIG. 12. *S. chinensis* var. *latus*. FIG. 13. *S. chinensis* var. *cuspidatus*. FIG. 14. *S. retusus*. All figures: leaves $\times \frac{3}{4}$, serrations $\times 1\frac{1}{2}$.

2. **Stachyurus obovatus** (Rehder) Li, comb. nov. *Stachyurus yunnanensis* Franch. var. *obovata* Rehder in Jour. Arnold Arb. **11**: 165. 1930; Hand.-Maz. Symb. Sin. **7**: 383. 1931. Figure 3.

A shrub, 1–3 m. tall, the branchlets olivaceous; leaves subcoriaceous, persistent, short-petiolate, greenish and slightly lustrous above, pale beneath, obovate, 5.5–7.5 cm. long, 2–3 cm. wide, the apex long-caudate-acuminate, the acumen 1–1.5 cm. long, the base narrowly attenuate, the margins slightly serrulate to subentire below, finely and sharply serrulate above, the teeth pointed, slightly callose, the lateral nerves about 5–7 on each side, subconspicuous above, elevated and prominent beneath, the tertiary veins inconspicuous on both surfaces; petioles about 0.5 cm. long; inflorescences spicate, short-pedunculate, 1–1.5 cm. long, the flowers sessile to subsessile, the bracts ovate, long-acuminate, about 1.5 mm. long, the bracteoles ovate, about 2 mm. long; sepals ovate, about 2 mm. long; petals ovate, 4–5 mm. long, 2–5 mm. wide; filaments about 4 mm. long; ovary and style about 4 mm. long, included, the stigmas ovate; fruit globose, about 7 mm. across, pedicellate, the pedicels 3–4 mm. long, articulate at the middle.

CHINA: SZECHUAN: Kuan Hsien, *W. P. Fang 2000, 12156, F. T. Wang 20504, 20618, Y. S. Liu 1856, C. S. Fan 81;* Mt. Omei, *W. P. Fang 3910, 7833, 6158, Y. S. Liu 1725, C. Y. Chiao & C. S. Fan 412;* Ping-shan Hsien, *F. T. Wang 22698.*

Professor Rehder states that "this plant looks at the first glance very distinct on account of its obovate almost lyrate caudate-acuminate leaves, but the leaves of some specimens of *S. yunnanensis* before me show a tendency toward an obovate shape and the serration agrees with that of *S. yunnanensis.* As the flowers are unknown, the specimens bearing young fruits, it does not seem wise to describe it as a new species." With adequate flowering material (*Fang 12156* and *Wang 22698*) and young fruiting material (*Wang 20504, 20618*) on hand, this writer is convinced that the variety deserves a specific standing. The leaves are not only distinctly and constantly obovate in shape, but they are also generally smaller than those of *S. yunnanensis* Franch. Moreover, the inflorescences are characteristically very short, scarcely exceeding 2 cm. long, and bearing only 3–8, rarely 10, flowers or fruits, and the styles are included, while in *S. yunnanensis* the inflorescences are 3–9 cm. long, bearing 12–22 flowers or fruits, and the styles are exerted.

3. STACHYURUS SALICIFOLIUS Franch. Jour. de Bot. **12**: 253. 1898; Chung, Mem. Sci. Soc. China **1**: 176. 1924. Figure 4.

A shrub, 1.5–3 m. tall, the branchlets olivaceous, glabrous; leaves chartaceous, glabrous, dark green above, pale beneath, linear-lanceolate, 8–15 cm. long, 0.7–1.7 cm. wide, the apex caudate-acuminate, the base obtuse, the margins inconspicuously serrulate, the teeth obtuse, incurved, the lateral nerves about 6–8 on each side, at first obliquely spreading, then abruptly ascending into longitudinal veins parallel to the midrib, their tips frequently joining the preceding lateral nerves, inconspicuous above, slightly elevated and conspicuous beneath, the tertiary veins inconspicuous on both surfaces; petioles short, 4–8 mm. long; inflorescences 5–7 cm. long, erect or pendulous, subsessile; flowers greenish white, subsessile or short-pedicellate, the bracts triangular-ovate, acuminate, about 2 mm. long, the bracteoles ovate, acute, about 2.5 mm. long; sepals ovate, about 4 mm. long, acute; petals obovate,

about 4 mm. long, 3–5.5 mm. wide, obtuse; filaments 5–6 mm. long; ovary and style about 6 mm. long, scarcely exerted, the stigmas capitate, distinct; fruit globose, about 4–6 mm. in diameter, with persistent style, the pedicels about 2.5 mm. long.

CHINA: SZECHUAN: Mt. Omei, *E. H. Wilson 4808, W. P. Fang 2720, 3186, 12890, T. T. Yü 409, 452, Y. S. Liu 1142*; Ping-shan Hsien, *F. T. Wang 22752, 22763.* YUNNAN: Tschen-fong-shan, *R. P. Delavay s.n.* (holotype, photo. and merotype in AA), July, 1894; Yi-liang Hsien, *H. T. Tsai 52118.*

This species is easily distinguished from the others by the long and narrow linear-lanceolate leaves with rather short petioles 4–5 mm. long.

4. STACHYURUS CORDATULUS Merr. Brittonia **4**: 122. 1941. Figure 5.

A shrub, subscandent, the branches glabrous; leaves chartaceous to coriaceous, glabrous, olivaceous on both surfaces to slightly paler beneath, oblong to oblong-lanceolate, 10–12 cm. long, 2.3–4 cm. wide, the apex subcaudately acuminate, the base slightly or distinctly cordate, the margins finely and sharply serrulate, the teeth pointed, spreading, about 0.5 mm. long, with callose apices, the lateral nerves 7 or 8 on each side, spreading, straight or slightly curved, united with longitudinal nerves located a little more than half way between the midrib and the leaf margins, subconspicuous above, distinct and elevated beneath, the tertiary veins inconspicuous on both surfaces; petioles 6–9 mm. long; inflorescences spicate, 4–9 cm. long, subsessile, the flowers greenish to slightly rosy, 5–6 mm. long, sessile, the bracts 1.5–2 mm. long, ovate at base, long-acuminate, the bracteoles ovate, about 2 mm. long, subacute to short-acuminate; sepals elliptic, concave, rounded, about 3 mm. long; petals obovate, rounded, about 5 mm. long and 3.5 mm. wide; filaments 1.5–2 mm. long; ovary ovoid, the style about 1 mm. long, the stigmas capitate, about 1 mm. in diameter.

BURMA: 'Nam Tamai at the Adung-Sienghku confluence, and along the Adung River, *K. F. Ward 9176* (paratype), *9191* (holotype), Jan. and Feb., 1931.

This distinct species is near to *Stachyurus himalaicus* Hook. f. & Thomson in the oblong-lanceolate leaves with fine and close serrations, but it is easily distinguished from the latter in that its leaves are shorter-petiolate, the base more distinctly cordate, the apex longer-acuminate, and the serrations straight, out-pointed, and more rigid. Moreover, the species is characterized by the venation, the straight or slightly curved lateral nerves being united directly with the nearly as prominent longitudinal pair, which is located a little more than half way between the midrib and the leaf-margins. A similar characteristic venation is found only in *S. salicifolius* Franch., but in that case the longitudinal veins are not always as distinct and sometimes are represented by extensions of the lower lateral veins not fully connected with the upper lateral ones. In other respects, *S. salicifolius* is readily distinguished from *S. cordatulus* by its very narrow linear-lanceolate leaves with acute bases and remote, obscure, and obtuse serrations.

5. STACHYURUS HIMALAICUS Hook. f. & Thomson ex Benth. Jour. Linn. Soc. Bot. **5**: 55. 1861; Thiselton-Dyer in Hook. f. Fl. Brit. Ind. **1**: 288. 1875; Rehder in Sarg. Pl. Wils. **1**: 287. 1912; Hayata, Ic. Pl. Formosan. **5**: 8. *f. 3.*

1915; Kanehira, Formosan Trees 62. *f.* 1917; Chung, Mem. Sci. Soc. China **1**: 176. 1924; Ito, Taiwan Shokubutu Dzusetu (Ill. Formosan Pl.) *pl. 464.* 1927; Chun, Sunyatsenia **1**: 275. 1934; Merr. Brittonia **4**: 121. 1941. *Stachyurus Sigeyosii* Masamune, Trans. Nat. Hist. Soc. Formosa **28**: 287. 1938, syn. nov. Figure 6.

A small tree with spreading branches, the branchlets chestnut-brown, with whitish lenticels; leaves chartaceous to coriaceous, glabrous, greenish above, pale beneath, oblong to oblong-lanceolate, 8–13 cm. long, 3.5–5.5 cm. wide, the apex long-caudate-acuminate, the base rounded to subcordate, the margins finely serrulate, the teeth minute, pointed, with callose apices, the lateral veins 5–7 on each side, ascending, elevated and prominent on both surfaces, the tertiary veins reticulate, subconspicuous on both surfaces; petioles 0.5–1.5 cm. long; inflorescences 5–10 cm. long, erect or pendulous, sessile, the flowers yellow, sessile, the bracts triangular-ovate, acuminate, about 2 mm. long, the bracteoles broadly ovate, acute, about 2 mm. long; sepals broadly ovate, obtuse, about 3 mm. long; petals obovate, rounded, 5 mm. long, 3.5 mm. wide; filaments 4–5 mm. long; ovary and style about 5 mm. long, scarcely exerted, the stigmas capitate; fruit subglobose, about 7–8 mm. across, subsessile to short-pedicellate, with short persistent style, the pedicels 2–3.5 mm. long, articulate at the middle.

CHINA: HUNAN: Sinning Hsien, *C. S. Fan & Y. Y. Li 608.* HUPEH: Chang-yang Hsien, *E. H. Wilson 192a;* no precise locality, *A. Henry 3449 A* (fragmentary). SZECHUAN: Mt. Omei, *Y. S. Liu 1670, C. Y. Chiao & C. S. Fan 387;* Kuan Hsien, Chien-chang Shan, *C. S. Fan 15.* SIKANG: Ya-an, *C. Y. Chiao 1925.* YUNNAN: no precise locality, *E. E. Maire 68, G. Forrest 9522, 9776, 16213, T. T. Yü 11434, H. T. Tsai 57266, 57599;* Mengtze, *A. Henry 10138, 10138A, 10543;* Niou-lou-kiang, *E. E. Maire 83;* between Schinlung and Ta Sung Shu, *C. Schneider 343;* Yunnanfu, *C. Schneider 378;* Ta Chang, *C. Schneider 749;* Likiang, *C. Schneider 2841, J. F. Rock 10575, G. Forrest 22221, C. W. Wang 70699, K. M. Feng 404, R. C. Ching 21595;* Tengyueh, *J. F. Rock 7994;* Champutong, Mt. Kenyichunpo, *J. F. Rock 11525;* Pe Yen Tsin, Son Pin Chao, *S. Ten 354, 364;* Ma-kwan Hsien, *H. T. Tsai 51851;* Shang-pa Hsien, *H. T. Tsai 54738;* Lan-ping Hsien, *H. T. Tsai 54047, 56283;* Lung-ling Hsien, *H. T. Tsai 56464;* Wei-si Hsien, *H. T. Tsai 63019, C. W. Wang 67900;* Champutong, *C. W. Wang 66709;* Kiukiang Valley, *T. T. Yü 19438;* Londjrela, *T. T. Yü 23147;* northern flank of Haba Snow Range, *K. M. Feng 1184;* southern Chungtien, *K. M. Feng 3087.* KWEICHOW: Fan Ching Shan, *Steward, Chiao, & Cheo 28.* KWANGSI: Ling-wan Hsien, *S. K. Lau 20458, Steward & Cheo 625;* Kwei-lin Hsien, Ma-wang-shan, *W. T. Tsang 28230, 28349.* KWANGTUNG: Pan Ling Tsze, *W. Y. Chun 5880;* Yang Shan Hsien, *T. M. Tsiu 741;* Loh-chang Hsien, Chong Uen Shan, *W. T. Tsang 20713, 20674.*

FORMOSA: No precise locality, *J. L. Gressitt 146;* Kuanania, *O. Warburg 10479;* Arisan, prov. Kagi, *E. H. Wilson 9752, 10799;* Horisha, prov. Nanto, *E. H. Wilson 10097;* Taiheisan, prov. Giran, *E. H. Wilson 10175, S. Suzuki s.n., K. Uno 10674;* Bankingin, *A. Henry 35;* Hassensan, *R. Kanehira 21190;* Sankyo, *K. Odashima 17850.*

INDIA: Eastern Himalaya, *K. Biswas s.n.*

BURMA: Above Zuklang, *F. K. Ward 427;* Adung Valley, *K. F. Ward 9297.*

This widely distributed species can be distinguished from *S. chinensis* Franch., another species of very wide distribution, by its longer but narrower, oblong or oblong-lanceolate leaves with fine and close serrations, and by the smaller flowers with the style scarcely exceeding the petals. Its inflorescence is also generally much longer. This writer has not been able to distinguish the Formosan *S. Siegeyosii* Masamune by its descriptions from

S. himalaicus especially from the Formosan plants of the latter species, and thus treats the former as a synonym of the latter.

6. STACHYURUS LANCIFOLIUS Koidz. Bot. Mag. Tokyo **32**: 135. 1918. *Stachyurus praecox* sensu Ito & Matsum. Tent. Fl. Lutch. **1**: 60. 1899, non Sieb & Zucc. Figure 7.

A shrub, 1.5–2.5 m. tall, the branchlets dark chestnut-brown, glabrous; leaves chartaceous, glabrous, lanceolate to ovate-lanceolate, rarely ovate-oblong, 12–19 cm. long, 3.5–7.5 cm. wide, the apex long-caudate-acuminate, the base rounded to subcordate, the margins finely serrulate, the teeth slightly incurved, obtuse, the lateral veins about 8 on each side, ascending, subconspicuous above, elevated and prominent beneath, the tertiary veins reticulate, inconspicuous above, subconspicuous beneath; petioles 3–5 cm. long; inflorescences 5–10 cm. long, sessile, pendulous, the flowers pale yellow, sessile, the bracts triangular-ovate, about 2 mm. long, acuminate, the bracteoles ovate, about 3 mm. long, obtuse; sepals ovate, about 4 mm. long; petals obovate to suborbicular, about 6–7 mm. long, 5–6 mm. wide, the apex rounded; filaments 3.5–4.5 mm. long; ovary and style about 3 mm. long, the stigmas capitate, distinct; fruit ellipsoidal, 9–12 mm. long, short-pedicellate.

JAPAN: Kyushu, *E. H. Wilson s.n.*, 3 collections; Liukiu Islands, *Yokohama Nursery Co., s.n.*

This species is close to *Stachyurus himalaicus* Hook. f. & Thomson in the oblong- or ovate-lanceolate finely serrulate leaves with rounded to subcordate bases, but differs in the longer petioles, slightly larger and more obtuse serrations, longer inflorescences with larger and more densely arranged flowers, and the larger fruits. The type is described from Kyushu, Japan, but no specimen is cited in the original description.

7. STACHYURUS MATSUZAKII Nakai, Bot. Mag. Tokyo **34**: 146. 1920. Figure 8.

A shrub about 5 m. tall, the branchlets stout, chestnut-brown dotted with white lenticels; leaves chartaceous, glabrous, greenish above, pale beneath, elliptic, 10–14 cm. long, 5–6.5 cm. wide, the apex long-acuminate, the base acute to rounded, the margins coarsely and prominently serrulate, the teeth large, obtuse, slightly incurved, with callose apices, the lateral nerves 5 or 6 on each side, ascending, subconspicuous above, elevated and prominent beneath, the tertiary veins reticulate, inconspicuous above, slightly conspicuous beneath; petioles 2.5–5 cm. long; inflorescences 4–12 cm. long, sessile, pendulous, the flowers sessile, light yellow, the bracts broadly triangular-ovate, about 2.5 cm. long, acuminate, the bracteoles ovate, about 3 mm. long, acute to obtuse; sepals ovate, about 3 mm. long, acute; petals 5–7 mm. long; fruits obovate-oblong, 13–15 mm. long, with short persistent styles.

JAPAN: Hondo, Shima, *Soemjima 9228.*

This species is characterized by its rather robust branches, long-petiolate and large leaves, which are coarsely serrulate, and the rather stout inflorescences. Two type collections are cited by Nakai, both from prov. Idzu, Hondo, the first from Hachijo Isnad, *T. Nakai & N. Matsuzakii s.n.*, and another from Oshima Island, *Saburo Okubo s.n.*

8. STACHYURUS MACROCARPUS Koidz. Bot. Mag. Tokyo **32**: 134. 1918. Figure 9.

A shrub, the branchlets dark chestnut-brown to blackish, glabrous; leaves chartaceous, glabrous and greenish above, pale beneath and slightly pubescent along the midrib and lateral nerves, soon glabrous, oblong to oblong-lanceolate, rarely ovate-elliptic to ovate-oblong, 7–14 cm. long, 3–5.5 cm. wide, the apex acuminate, the base rounded to obtuse, the margins obtusely and rather broadly serrulate, the teeth slightly incurved, with callose apices, the lateral nerves about 6 on each side, ascending, subconspicuous above, elevated and distinct beneath, the tertiary veins reticulate, inconspicuous above, subconspicuous beneath; petioles 2–5 cm. long; inflorescences 3.5–4 cm. long, subsessile, the flowers subsessile, rather densely arranged, the bracts broadly triangular-ovate, about 2 mm. long, acuminate, the bracteoles ovate, obtuse, about 2.5 mm. long; sepals ovate, about 3 mm. long; petals obovate, obtuse, about 5 mm. long and 3 mm. wide; filaments about 4 mm. long; ovary and style about 4 mm. long, the stigmas capitate, distinct; fruit oblong, 18–20 mm. long, 12–16 mm. wide, subsessile.

BONIN ISLANDS: No precise locality, *Hidemasa Otorno s.n.*, 2 collections.

This species is characterized by its oblong to oblong-lanceolate and acuminate leaves with remote and obtuse serrations, rather short inflorescences about 3.5–4 cm. long, and large fruits up to 2 cm. long. The type specimen is *S. Nishimura 105* from Chichishima Island, Bonin.

8a. STACHYURUS MACROCARPUS Koidz. var. PRUNIFOLIUS Tuyama, Bot. Mag. Tokyo **53**: 7, (as *purnifolius*). 1939.

Differs from the species in the thinner leaves with smaller, closer, acute serrations, and more numerous lateral nerves, about 9–11 on each side.

Recorded by T. Tuyama from Bonin Islands (type specimen: Hahazima Island, *T. Tuyama s.n.*); no specimen seen by this writer.

9. STACHYURUS PRAECOX Sieb. & Zucc. Fl. Japon. **43**: *pl.* 18. 1835; Abh. Math.-Phys. Cl. Bayer. Akad. Wiss. **4** (2): 152. 1845; Franch. & Sav. Enum. Fl. Jap. **1**: 59. 1875; Carrière, Rev. Hort. **1869**: 200. *f. 49.* 1869; Rouhard, Rev. Hort. **1908**: 86. *f. 28, 29.* 1908; Hook. Bot. Mag. **108**: *pl. 6631.* 1882; K. Ito, Fig. & Descr. Pl. Koishik. Bot. Gard. **2**: *pl. 22.* 1883; Lauche, Deutche Dendrol. ed. 2: 413. *f. 163.* 1883; Nicholson, Ill. Dict. Gard. 3: 483. *f. 518.* 1887; Bull. Coll. Agric. Tokyo **2**: *pl. 7, f. 21.* 1895; Gard. Chron. III. **21**: *f. 97.* 1897; Shirasawa, Ic. Ess. Forest Jap. **1**: *pl. 74.* 1900; Schneider, Dendrol. Winterst. 86. *f.* 1903; Ill. Hand. Laubh. **2**: 363. *f. 241a–b, 245.* 1909; Dallimore, Gard. Chron. III. **43**: 196. *f. 83.* 1908, 49: 213. 1911; Miyoshi, Pl. World. Jap. 128: *f.* 1917; Osborn, Garden **75**: 204. *f.* 1911; Gard. Chron. III. **79**: 229. 1926; Bean, Trees & Shrubs **2**: 545. *f.* 1914; Rehder in Bailey, Stand. Cycl. Hort. **6**: 3221. *f. 3674.* 1917; Man. Cult. Trees & Shrubs 640. 1927; ed. 2, 654. 1940. *Stachyurus japonicus* Steud. Nom. ed. 2, **2**: 630. 1841, sphalm. Figure 10.

A shrub, 1–4 m. tall, the branches spreading, the branchlets reddish brown or chestnut-brown, lustrous, glabrous; leaves chartaceous, greenish, lustrous and glabrous above, pale and slightly pubescent along the midrib and lateral nerves beneath, soon glabrous, elliptic-ovate to ovate-lanceolate, 7–15 cm.

long, 3.5–6.5 cm. wide, the apex long-acuminate, the base rounded to subcordate, the margins serrulate, the teeth slightly spreading, the lateral nerves about 5 or 6 on each side, ascending, more or less elevated and prominent on both surfaces; petioles 2–5 cm. long; inflorescences 5–9 cm. long, sessile to subsessile, erect or pendulous, the flowers yellow, sessile, the bracts broadly ovate, acute, about 2 mm. long, the bracteoles broadly ovate, obtuse, about 2 mm. long; sepals broadly ovate, acute, about 3 mm. long; petals obovate, 6–7 mm. long, 4–5 mm. wide; filaments 4–5 mm. long; ovary and style 4–5 mm. long, included, the stigmas capitate, distinct; fruit globose, about 8 mm. long, with or without persistent styles, short-pedicellate, the pedicels 1.5–2 mm. long, articulate at the middle.

JAPAN: No precise locality, *Faurie 6128*, *H. Kuenberg 2840a*; Hokkaido, prov. Oshima, *K. Miyabe & Y. Tokubuchi s.n.*; Hokkaido, *C. S. Sargent s.n.*; Hokkaido, Kakkumi Hot Spring, *C. S. Sargent s.n.*; Atami to Odawara, *C. S. Sargent s.n.*; Miyanoshita, *C. S. Sargent s.n.*; Hondo, Shinano prov., *E. H. Wilson s.n.*; Hondo, Safami prov., *E. H. Wilson s.n.*; Hondo, Mino prov., *K. Shiota 340*, *8055*, *9683*; Kyushu, Nagasaki, *E. H. Wilson s.n.*; Kyushu, Mt. Kirishima, *E. H. Wilson s.n.*; Nokogiriyama, prov. Awa, *K. Miyabe s.n.*; Chikugo, *H. Mayr s.n.*; Nikko, *N. Mochizuki s.n.*; Mt. Amgi, *Sci. Coll. Imp. Univ. s.n.*; Iyo, *K. Sakurai s.n.*; between Shojiko and Kofu, *P. H. Dorsett & W. J. Morse 561*, Kobe, Rokkosan, *K. Uno 13656*; Ikerigaseki, Aomoriken, *K. Uno 2597*.

A species of common and wide occurrence in Japan, now frequently cultivated for its flowers. Siebold and Zuccarini, in their original description of the genus and the species, mention that the plant is common in Japan, but cite no specimen.

10. STACHYURUS CHINENSIS Franch. Jour. de Bot. **12**: 254. 1898; Diels, Bot. Jahrb. **92**: 475. 1900; Lecomte, Fl. Gén. Indo-Chine **1**: 353. *f. 33, 12–18.* 1910; Rehder in Sarg. Pl. Wils. **1**: 287. 1912; in Bailey, Stand. Cycl. Hort. 6: 3221. 1917; Jour. Arnold Arb. **8**: 178. 1927; Man. Cult. Trees & Shrubs 641. 1927; ed. 2, 654. 1940; Bean, Gard. Chron. III. **58**: 147. *f. 47.* 1915; Garden **79**: 182 *f.* 1915; Bowles, Garden **82**: 161. *f.* 1918; Chun, Mem. Sci. Soc. China **1**: 176. 1924; Osborn, Gard. Chron. III. **79**: 229. *f. 113.* 1926; Kirk, Brit. Gard. Flora 129. *f. 45.* 1927; Merr. Lingnan Sci. Jour. **7**: 316. 1931; Hand.-Maz. Symb. Sin. **7**: 383. 1931; Ganteau, Rev. Hort. **1932**: 95. *f. 33.* 1932. *Stachyurus praecox* sensu Diels, Bot. Jahrb. **29**: 475. 1900, non Sieb. & Zucc. *Stachyurus Duclouxii* Pitard ex Chung, Mem. Sci. Soc. China **1**: 176. 1924, nomem nudum, syn. nov. Figure 11.

A shrub, 3–5 m. tall, the branchlets dull brownish, with scattered whitish lenticels, glabrous; leaves chartaceous to membranaceous, greenish and glabrous above, pale and glabrous and slightly pubescent along the midrib and lateral nerves beneath, soon glabrous, ovate to ovate-oblong, 6–12 cm. long, 2.5–7.5 cm. wide, the apex more or less abruptly long-acuminate, the base rounded to subcordate, the margins crenate-serrulate, the lateral nerves 5 or 6 on each side, elevated and conspicuous on both surfaces, the tertiary veins reticulate, subconspicuous to conspicuous on both surfaces; petioles 1–2 cm. long; inflorescences 6–13 cm. long, sessile, the flowers yellow, subsessile or short-pedicellate, the bracts triangular-ovate, acuminate, about 2.5 mm. long, the bracteoles ovate, acute, about 3 mm. long; sepals ovate, obtuse, about 3.5 mm. long; ovary and style 6–7 mm. long, exerting the

petals, the stigmas capitate, distinct; fruit globose, about 6 mm. in diameter, with or without persistent styles, short-pedicellate, the pedicels about 1.5 mm. long.

CHINA: HUNAN: Hsinhwa, Hsikwanshan, *H. Handel-Mazzetti 582=11763;* Yi-chang Hsien, Ping Ton Shan, *W. T. Tsang 23528.* HUPEH: no precise locality, *A. Henry s.n.;* Ichang, *E. H. Wilson 89, 125;* Chang-yang Hsien, *E. H. Wilson 192;* Hsing-shan Hsien, *E. H. Wilson 2556;* Gian Gia-kou, *W. Y. Chun 3585;* Tan Shu Ya, *W. Y. Chun 4408;* Siu Jeh-su, *W. Y. Chun 4415;* Patung Hsien, *H. C. Chow 63.* SZECHUAN: No precise locality, *A. Henry 5744;* Chung-hsien, *W. P. Fang 506;* Nanchuan Hsien, *C. Bock & A. Rosthorn 2000, W. P. Fang 1064;* Kuan Hsien, *W. P. Fang 2211, S. S. Chien 5117, F. T. Wang 20496, 20583;* Lishui Hsien, *W. P. Fang 20;* Opien Hsien, *W. P. Fang 7238, Y. S. Liu 1999;* Mt. Omei, *W. P. Fang 2392, 2466, 2589, 3042, 3207, F. T. Wang 23219a, Y. S. Liu 1207, T. T. Yü 386, 448, S. S. Chien 5543;* Hung-ya Hsien, *W. P. Fang 7977, 8117, 8518, 8636;* Ma-pien Hsien, *W. P. Fang 4607;* Chenk-kou Hsien, *W. P. Fang, 10049;* Han-yuan, *W. C. Cheng 649, 669;* Mao Hsien, *F. T. Wang 21943;* Kwang-yun Hsien, *F. T. Wang 22638;* Ping-shan Hsien, *F. T. Wang 22703;* Ma-pien Hsien, *F. T. Wang 22857;* Lololand, between Alami and Ssuqueh, *C. Schneider 927;* between Oti and Quentin, *C. Schneider 1389.* SIKANG: Dzer-nar, Tsa-wa-rung, *C. W. Wang 66318, 66356, 66389, 66392;* Kanting, near Wu Ya Ling, *C. Y. Chiao 1741.* YUNNAN: No precise locality, *G. Forrest 10143, 10245, H. T. Tsai 57320, T. T. Yü 10259;* Longki and Tchan-fong-shan, *R. P. Delavay s.n.* (holotype, photo. and merotype in AA); Suen-oui, *E. E. Maire 79;* Cai-pou, *E. E. Maire 146;* Likiang, *C. Schneider 2930, 3498, J. F. Rock 4059, 8059, 8541;* Chao-tung Hsien, *H. T. Tsai 50899;* Cheng-hsiung Hsien, *H. T. Tsai 52305;* Ping-pien Hsien, *H. T. Tsai 62297, 62613;* Shang-pa Hsien, *H. T. Tsai 54805, 59103, 56542;* Chi-tze-lo, *H. T. Tsai 54189, 58558;* Wei-si Hsien, *C. W. Wang 63031, 63589, 63694, 64055, 68084;* Champutong, *C. W. Wang 66682;* Atungtze, Mt. Kakerpu, *T. T. Yü 10322;* Shunning, Hila, *T. T. Yü 16474;* southern Chungtien, Anangu, *K. M. Feng 1011.* KWEICHOW: Tsungyi Hsien, *Steward, Chiao, & Cheo 32;* Kweiyang, *S. W. Teng 90041.* KWANGSI: Northern Luchen, Chufeng-shan, *R. C. Ching 5782;* northern Hin Yen, Yeo Mar Shan, *R. C. Ching 7154;* Chuen Yuen, *Z. S. Chung 82022.* KWANGTUNG: Lohchang Hsien, *Y. Tsiang 1373, 1399;* Yu-yuen, *S. P. Ko 9192, 52562.* FUKIEN: No precise locality, *Hongk. Herb. 2403;* Pu-cheng, *R. C. Ching 2503.* (Also recorded from Shensi, Anhwei, Chekiang, and Kiangsi (Rehder l.c., Merrill, l.c.).

INDO-CHINA: Tonkin, Chapa, *A. Petelot 5690.*

This species of very wide distribution is close to the common Japanese species *S. praecox* Sieb. & Zucc., but may be distinguished by the broader and more abruptly acuminate leaves, the relatively longer petioles, the shorter pedicels in the fruit, and the smaller fruit. The leaves of *S. praecox* are more oblong and longer acuminate.

A photograph taken by Professor Rehder from the type specimen of *Stachyurus Ducloxii* C. J. Pitard in the Paris Museum (Yunnan: Hay tien, *Fr. Ducloux 2367*, March, 1904), which apparently has never been published, together with fragments of leaves and inflorescences, are found in the herbarium of the Arnold Arboretum. The name is listed in Chung's Catalogue of Trees and Shrubs of China (l.c.), probably being based on this particular photograph. The specimen is a flowering plant with juvenile leaves. It apparently represents *S. chinensis* Franch.

Stachyurus chinensis is quite variable in the size, shape, and serration of the leaves. These variations, however, although manifest in some cases, are gradual and inconstant. The species as a whole is generally easily recognizable and distinguishable from other species. The following varieties are recognized.

10a. STACHYURUS CHINENSIS Franch. var. **latus** Li, var. nov. Figure 12.

A typo speciei differt foliis plerumque latioribus, tenuiorbius, 6–7.5 cm. longis, 5–6.5 cm. latis, suborbicularibus vel ovatis, basi distincte cordatis, margine crasse serrulatis, apice abrupte acuminatis, acumine 5–8 mm. longo.

CHINA: ANHWEI: Chiuhwashan, *S. C. Sun, 1216.* HONAN: Sunghsien, San Kuan Miao, *J. Hers 1305* (TYPE), Sept., 1919. HUPEH: Feng Hsien, *E. H. Wilson 292;* Wan Tsao Shan, *W. Y. Chun 3901, 3956;* Hsin Tien Tsze, *W. Y. Chun 4039, 4041;* Huan Tsao, *W. Y. Chun 4138.* SZECHUAN: Nanchuan Hsien, *C. Y. Hwang 99, W. P. Fang 830, 920, 1024, 1402, 5528;* Cheng-kou Hsien, *W. P. Fang 10309.*

This variety is found in the provinces along the Yangtze Valley and north of it. The typical form of the species is found mainly in the southern provinces. The Honan and Anhwei specimens of this variety are clearly different from the typical form, while plants from western Hupeh and Szechuan, where the typical form is also located, are in some instances without very sharp distinction. The typical form, occurring in the south, is nearer to *S. himalaicus* Hook. f. & Thomson both geographically and structurally in the shape and serrations of the leaves than this variety.

It could be mentioned in this connection that specialization in the shape and serrations of the leaves in the genus is clearly traceable, as illustrated by the figures, from *S. himalaicus*, with oblong-ovate, acuminate, finely serrulate leaves, to *S. chinensis*, then to *S. chinensis* var. *latus* and *S. chinensis* var. *cuspidatus*, finally to *S. retusus*, with orbicular, emarginate, cordate leaves with much coarser serrations.

10b. STACHYURUS CHINENSIS var. **cuspidatus** Li, var. nov. Figure 13.

A typo speciei differt foliis suborbicularibus, 6.5–7.5 cm. longis, 5.5–6.5 cm. latis, basi rotundatis vel cordatis, apice latis, cuspidato-emarginatis, acumine lineari, 1–1.5 cm. longo, 0.3–0.5 cm. lato, interdum nullo.

CHINA: SZECHUAN: West of Wen-chuan Hsien, *W. P. Fang 20945* (TYPE), May 21, 1931.

11. STACHYURUS RETUSUS Yang, Contr. Biol. Lab. Sci. China **12**: 105. *pl. 6.* 1939. Figure 14.

A shrub, about 3 m. tall, the branchlets dark olivaceous, covered sparsely with white lenticels; leaves chartaceous, green, lustrous, and glabrous above, pale, white, tomentose to glabrous beneath, orbicular-oblong, 4.5–8 cm. long, 4–8 cm. wide, the apex retuse, rarely truncate or bilobed, the base cordate, the margins serrulate, the teeth obtuse, slightly incurved, the lateral nerves 5 or 6 on each side, ascending, elevated and prominent on both surfaces, the tertiary veins reticulate, conspicuous on both surfaces; petioles 1.5–2.3 cm. long; inflorescences (immature) to 4 cm. long, pendulous, subsessile, the bracts broadly triangular-ovate, about 2 mm. long, acuminate, the bracteoles 2, the flower buds sessile, the style very short, the stigmas globose, 4-lobed.

CHINA: SZECHUAN: Mt. Omei, *F. T. Wang 23248.*

This species is characterized by its suborbicular leaves, which are emarginate or bilobed at the apex and cordate at the base. Yang, basing on *C. W. Yao 3365* from Mt. Omei, Szechuan, describes the lower surface of the leaves as being densely covered with white hairs, which are not observed in the

above cited specimen, but which may be present on younger specimens and falling off in age as in some other species of the genus. The specimen cited, collected from the type locality, bears also immature racemes like the type and therefore no additional data could be added. The leaves are more or less chartaceous, in size and serration closely resembling those of *S. chinensis;* the general shape resembles especially that of var. *latus*. Apparently the leaf represents further specialization resulting in the disappearance of the acumen of var. *cuspidatus*. Occasionally an emarginate leaf like that of this species can also be found on a few specimens of *S. chinensis*. More material, particularly mature flowering and fruiting specimens, is needed for study in order to decide whether it is best to treat this as a variety of *S. chinensis* or to retain it as specifically distinct from the latter.

12. STACHYURUS OVALIFOLIUS Nakai, Jour. Jap. Bot. **15**: 534. 1939.

A shrub, 3–6 m. tall, the branches pale brownish to red-brownish; leaves ovate to broadly ovate to cordate-ovate, green and glabrous above, pale and sparsely pilose along the nerves or glabrous beneath, 7–12 cm. long, 5–7 cm. wide, the apex cuspidate, the base rounded or cordate to truncate, the margins coarsely mucronate-serrulate; petioles 1–5 cm. long; inflorescences racemose, dioecious, the male 7–12 cm. long, the female 3–7 cm. long, glabrous, the bracts deciduous; sepals and petals 4, distinctly imbricate; stamens 8, in 2 series, in male flowers 6–7 mm. long, in female flowers 3 mm. long, the anthers ovate-rounded; ovary ovate, the base pilose, the style 2–2.5 mm. long, the stigmas capitate; fruits about 15 mm. long, oblong to oblong-pyriform, with persistent style.

This species is described by Nakai from Hondo, Japan, and based on seven collections (Prov. Sagami, Enosima, *T. Nakai s.n.*, 2 coll., *Yasu-iti Momiyama s.n.*, 2 coll., Hayakawa, *Kiyotaka Hisanti s.n.;* Prov. Izu, Osima, *T. Nakai s.n.;* between Yawatano and Naramoto, *T. Nakai s.n.*). No specimen has been seen by the writer. Nakai mentions: "affinis *S. praecox* et *S. Matsuzakii*, sed a priori foliis sæpe cordato-ovatis grossius serratis, floribus viridulis vel viridi-flavascentibus majoribus, fructibus oblongis vel pyriformibus; et a posteriori caule fruticoso, foliis brevibus cordato-ovatis distinctus est." Again at the end of the description he notes that "this is a coastal plant, easily distinguishable from *S. praecox* by its more vigorous growth, more reddish branchlets, larger shining leaves, longer spikes, and larger paler flowers." From Nakai's original description, the species appears to be particularly close to *S. Matsuzakii* Nakai. As no specimen is available for study, this species is not incorporated in the key.

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THE SEPARATION OF ERIGERON FROM CONYZA

ARTHUR CRONQUIST

The preparation of a revision of the North American species of *Erigeron*, in which I am currently engaged, necessitates a careful delimitation of the genus. As is well known, it passes on the one hand into *Aster* and on the other into *Conyza*. In distinguishing it from *Aster*, I have found necessary only minor changes, involving individual species. Its present separation from *Conyza* is much less satisfactory, however, and merits detailed consideration.

The genus *Conyza*, as now commonly treated, differs from *Erigeron* in having no ligules at all on the numerous multiseriate pistillate flowers. This despite the fact that Bentham and Hooker[1] admit that *Conyza* may sometimes have narrow ligules shorter than the styles, and indicate that *C. absinthiaefolia* DC. sometimes has short ligules and sometimes lacks them. Bentham,[2] in a classic paper on *Compositae*, says: "To distinguish, however, *Conyza* and *Erigeron* from *Aster*, we have but little besides the increase in number and reduction in size of the female florets, which in *Erigeron*, although they have still the corollas produced into a ligula, have that ligula always very narrow, and often short; whilst in *Conyza* these corollas are still further reduced to a filiform tube, shorter than the style, toothed or truncate at the top, the ligula remaining undeveloped." A few pages farther on he says of the female florets of *Conyza*, "rarely producing a small scarcely spreading ligula."

The genus *Erigeron* usually has numerous central hermaphroditic flowers, and from few to numerous pistillate flowers with well-developed ligules. In some species the ligules are short or even absent, but the heads seem otherwise unaltered. The tubular pistillate corollas merely lack ligules. Several ordinarily ligulate species have eligulate forms of this type.

In the section *Trimorphaea* (included in *Euerigeron* by Bentham), the most common species of which is *E. acris* L., the corollas of the outer pistillate flowers are very slender and bear short filiform ligules which sometimes do not exceed the pappus. Usually there is an inner series of pistillate flowers with no ligules at all. Here we have an obvious approach toward the *Conyza* type, there being needed to complete the transition merely the disappearance of the already filiform and short ligules, and some decrease in the number of central hermaphroditic flowers. *Trimorphaea* is inextricably bound to *Erigeron*, however, by the obvious evolutionary line of *E. simplex* Greene, *E. uniflorus* L. (*sens. lat.*), and *E. alpinus* L., in which *E. simplex*

[1] Gen. Plant. **2**(1): 283. 1873.

[2] Jour. Linn. Soc. **13**: 335–577. 1873.

is true *Erigeron*, *E. alpinus* is *Trimorphaea*, and *E. uniflorus* is somewhat intermediate.

The next step in the progression toward *Conyza* is furnished by the section *Coenotus*, the most common species of which is *E. canadensis* L. The generic names *Leptilon* Raf. and *Conyzella* Rupr. have sometimes been used for this group by those who were unwilling to include it in *Erigeron* but not bold enough to transfer it to *Conyza*. *Coenotus* differs from *Trimorphaea* in having the central hermaphroditic flowers usually fewer, the pistillate flowers comparatively more numerous, and the ligules reduced so that to casual inspection the heads appear discoid. In the words of Asa Gray,[3] the narrow ligule is "always short · than its tube, often shorter than the style branches, or even obsolete." Be it noted again that Bentham and Hooker allowed the presence of ligules shorter than the style branches in *Conyza*.

The differences between *Coenotus* and *Trimorphaea* are not great, but the species of the two groups do not seem intimately related. *E. canadensis*, the most nearly bridging species of the section, is scarcely confusable with any species of *Trimorphaea*. Although it is reported to produce a sterile hybrid with *E. acris*,[4] no one familiar with the two species would consider them very closely related.

From *Coenotus* to true *Conyza*, with no ligules at all, is an easy step, as Gray[3] further indicates by the statement, "with the aspect of *Conyza*, and passing into that genus."

Superficially, it seems reasonable to include in *Erigeron* all the species which have any ligule at all, and restrict *Conyza* to the entirely eligulate species. This has been the general practice, despite the fact that Bentham and Hooker admitted to *Conyza* some species with tiny ligules. Unfortunately, the resulting generic segregation is highly artificial. Species which are obviously related to true *Conyza* species, and which have every external appearance of *Conyza*, are found to have tiny ligules, and are thus placed in *Erigeron*. We have *Erigeron microglossus* Blake,[5] the describer of which said, "The species, although of Conyzoid appearance, is technically a true *Erigeron* in the presence of a definite although minute ligule." The ligule is described as being 0.3 mm. long! We have *Conyza mima* Blake,[5] of which Blake said, "The species is named from its great resemblance to *Erigeron subspicatus* Benth., a resemblance so close that except in technical characters of the head the two species can scarcely be distinguished." We have the paired species *Erigeron gnaphalioides* HBK. and *Conyza gnaphalioides* HBK., much confused in herbaria and distinguished chiefly by the fact that the former has tiny ligules. *Conyza Coulteri* Gray is similarly confused with *E. Schiedeanus* Less., for which Gray himself at first mistook it.

[3] Syn. Fl. N. Am. **1**(2): 220. 1884.

[4] Vierhapper, F. Monographie der Alpinen *Erigeron*—Arten Europas und Vorderasiens. Beih. Bot. Centralbl. **19**(2): 385–560. 1906.

[5] Contr. Gray Herb. II. **3**(52): 16–59. 1917.

Descriptions of new tropical species, of Conyzoid aspect, but referred to *Erigeron* because they possess minute ligules, continue to appear intermittently in scientific journals. Long-accepted species of *Conyza* (e.g., *Conyza notobellidiastrum* Griseb.) are transferred to *Erigeron* because the outer florets are found to possess minute ligules. The Gray Herbarium Card Index lists an even dozen South and Central American species of *Conyza* that have been transferred to *Erigeron*. No doubt a thorough inspection of the genus would reveal that other plants still reposing peacefully as species of *Conyza* possess more or less definite ligules. Furthermore, it seems not unlikely that field study of species now known chiefly from herbarium sheets would show some of them to be not entirely constant in the matter of ligules, placing them in company with *C. absinthiaefolia*.

If our taxonomic system is to be merely a series of convenient pigeonholes whereby plants may be catalogued, we may well distinguish *Erigeron* from *Conyza* by the presence of a ligule, even if it be microscopic. We should then dismember the species which may or may not have ligules, placing the ligulate individuals in one genus, and the eligulate individuals in the other. If, however, we hope to arrive at a natural arrangement, we must seek farther for our distinction.

In surveying the numerous species which link true *Erigeron* to true *Conyza*, we find that in only one place is there any suggestion of a real break. That is between *Trimorphaea* and *Coenotus*. Here at least we are not reduced to separating into different genera species which are almost indistinguishable. I therefore propose that the section *Coenotus* be transferred in toto to *Conyza*, and expanded to include all the species of the genus which ordinarily possess ligules.

Conyza and *Erigeron* are redefined as follows:

Conyza: Central hermaphrodite flowers few; pistillate flowers numerous, with filiform corollas; ligules, if present, inconspicuous, shorter than the tubes and scarcely if at all exceeding the pappus.

Erigeron: Central hermaphrodite flowers many, or sometimes rather few; pistillate flowers few to numerous, sometimes with filiform corollas, but then the outer at least with definite ligules equalling or surpassing the pappus.

Even as redefined, the two genera are not sharply distinct, as will be noted from the foregoing characterizations. In America, little or no trouble will be encountered in placing any particular species in the proper genus. In the old world it may sometimes be more difficult, for it is there that the section *Trimorphaea* reaches its greatest development. I believe that the most satisfactory procedure, in any doubtful case, will be to refer the species in question to the genus to which its nearest relatives belong. In some cases this may necessitate considerable study, but the result will be a more nearly natural delimitation of the genera involved. Precisely the same type of situation exists in distinguishing *Erigeron* from *Aster*. It has already in some

cases been met in the fashion here proposed, by referring the species to the genus to which its nearest relatives belong. *Erigeron peregrinus* (Pursh) Greene, for example, is correctly treated by almost all modern American botanists as being an *Erigeron* rather than an *Aster*, because it is closely related to undoubted species of *Erigeron*, although on the basis of technical characters it might better be placed in *Aster*.

Some minor points which may have some bearing may be mentioned. The genus *Conyza* is largely tropical, and according to Bentham (2), "ranges over the warmer regions of Asia, Africa, and America." Further, Bentham says, "*Euerigeron* . . . belongs to the northern hemisphere, and is chiefly mountainous. . . . *Coenotus*, the section which passes into *Conyza*, is now pretty nearly cosmopolitan, and like *Conyza*, overruns tropical as well as temperate regions, the preponderance of local species being African as well as American. . . . The well known *E. canadensis* . . . is almost intermediate between *Coenotus* and *Euerigeron*." Thus we see that in distribution *Coenotus* is more nearly like true *Conyza* than like true *Erigeron*. The weedy habit of *E. canadensis* is quite in keeping with that of some species of true *Conyza*. Furthermore, the species (*E. canadensis*) which is most nearly intermediate between *Coenotus* and true *Erigeron* is certainly of Conyzoid aspect, and does not seem closely related to any species of undoubted *Erigeron*.

I shall publish formal transfers for only a few American species. The rest I leave to others who may be more conversant than I with the individual species concerned.

Conyza araneosa (Urb.) Cronquist, comb. nov. *E. arancosus* Urb. Symb. Antill. **3**: 404. 1902.

Conyza bonariensis (L.) Cronquist, comb. nov. *E. bonariensis* L. Sp. Pl. **2**: 863. 1753.

Conyza canadensis (L.) Cronquist, comb. nov. *E. canadensis* L. Sp. Pl. **2**: 863. 1753.

Conyza confusa Cronquist, nom. nov. *E. gnaphalioides* HBK. Nov. Gen. **4**: 88. *pl. 331.* 1820. Not *Conyza gnaphalioides* HBK.

Conyza eriophylla (Gray) Cronquist, comb. nov. *E. eriophyllus* Gray, Pl. Wright. **2**: 77. 1853.

Conyza microglossa (Blake) Cronquist, comb. nov. *E. microglossus* Blake Contr. Gray Herb. II. **3**(52): 31. 1917.

Conyza parva Cronquist, nom. nov. *E. pusillus* Nutt. Gen. **2**: 148. 1818. Not *Conyza pusilla* HBK.

Conyza ramosissima Cronquist, nom. nov. *E. divaricatus* Michx. Flor. Bor.-Am. **2**: 123. 1803. Not *Conyza divaricata* Spreng.

Conyza Schiedeana (Less.) Cronquist, comb. nov. *E. Schiedeanus* Less. Linn. **5**: 145. 1830.

Conyza subspathulata Cronquist, nom. nov. *E. spathulatus* Vahl. in West, Bidrag Ste. Croix. 303. 1793. Not *Conyza spathulata* Hornem.

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SUPPLEMENTARY NOTES ON THE AMERICAN SPECIES OF ERYTHRINA—II

B. A. KRUKOFF

Through the courtesy of the curators of the botanical institutions mentioned below I was privileged recently to study their collections of *Erythrina*. Many of these collections are not represented by duplicates in American and European herbaria. Extensive collections of *Erythrina* by Drs. Paul C. Standley and Julian A. Steyermark recently made in connection with their work on the flora of Guatemala also became available to me.

Dr. Karl Folkers, Mr. J. Shavel, Jr., and Mr. F. Koniuszy of the Merck Research Laboratory have continued their studies of the alkaloids derived from seeds of various species of *Erythrina* (1, 2, 3) whereas Dr. E. S. Harrar of Duke University has recently undertaken a study of the wood anatomy of species of this genus. In connection with these studies a number of specimens have been received for identification.

The collections examined extend our knowledge of certain species previously known from incomplete material, and extensions of ranges are noted for a number of species. No changes in the nomenclature are necessitated.

The species are arranged in the same order, and the place of deposit of specimens is shown by the same abbreviations as used in my previous papers on *Erythrina* (4, 5). The following new abbreviations are used:

Geor: Georgetown Botanic Garden, British Guiana.
Trin: Trinidad Botanical Garden, Port of Spain.
CR: Museo Nacional de Costa Rica, San Jose.
Cuz: Universidad del Cuzco, Peru.

1. ERYTHRINA GLAUCA Willd.

TRINIDAD: cultivated: *Bot. Gard. Trin. 8353* (Trin). COSTA RICA: Puntarenas: *Brenes 3855* (CR). PANAMA: Canal Zone: *White & White 62* (M). Panama: *Allen 1628* (GH, M). COLOMBIA: Valle del Cauca: *Ramos Nunez s.n.* (*Kr. Herb. 15191*). Huila: *Plata Garcia 45* (Col). VENEZUELA: Carabobo: *L. Williams 12336* (F). Apure: *L. Williams 12961* (F, NY). Federal District: *Tamayo 1284* (F, NY); *Brother Elias 138* (A). Bolivar: *L. Williams 12560* (F, NY,A). ECUADOR: Guayas: *Mille s.n.* (*Kr. Herb. 15350*). PERU: Loreto: *Fernandez s.n.* (*Kr. Herb. 15255*). BRITISH GUIANA: Demerara: *Jenman 3946* (Geor).

Local names: Porotillo (Ecuador); Pisamo (Colombia).

The Brenes' specimen is the first record of the species from the province of Puntarenas, the Williams' specimen—from the State of Apure. The collector states on the label (*Tamayo 1284*): "Las flores son comidas por los pájaros llamados 'arrendajos'. Habiendo leído no se si en la relación del

gobernador Pimentel (15. .) que los Indios del valle de Caracas comían la flor del bucare."

2. ERYTHRINA CRISTA-GALLI L.

TRINIDAD: cultivated: *Bot. Gard. Trin. 12729* (Trin). COSTA RICA: San Jose: cultivated: *J. Valerio 1398* (CR). ARGENTINA: *Santini s.n.* (*Kr. Herb. 15233*). Tucuman: *Meyer s.n.* (*Kr. Herb. 15098*).

3. ERYTHRINA FALCATA Benth.

PERU: Cuzco: *C. Vargas C. 2943* (Cuz). BRAZIL: Minas Geraes: *Mello Barreto 1999* (F). ARGENTINA: Buenos Aires: cultivated: *Thays s.n.* (*Kr. Herb. 15396*). Salta: *Meyer 35390.*

4. ERYTHRINA POEPPIGIANA (Walp.) O. F. Cook.

TRINIDAD: cultivated: *Bot. Gard. Trin. 1332* (Trin), *7574* (Trin), *11947* (Trin), *13325* (Trin). NICARAGUA: Managua: cultivated: *Garnier s.n.* COSTA RICA: Cartago: cultivated: *Jorge Leon 769* (CR). COLOMBIA: Valle del Cauca: *Ramos Nunez s.n.* (*Kr. Herb. 15192*). Boyaca: *Cuatrecasas 9676* (US). Putumayo: *Cuatrecasas 11372* (US). VENEZUELA: Carabobo: *L. Williams 12332* (in part, F). Federal District: *Tamayo 1285* (F), *1309* (NY, US).

The Cuatrecasas' specimens are the first record of the species from Boyaca and Putumayo.

6. ERYTHRINA DOMINGUEZII Hassler.

ARGENTINA: Jujuy: *Fawcett s.n.* (*Kr. Herb. 15394*). Chaco: *A. Schulz s.n.* (*Kr. Herb. 15126*), *s.n.* (*Kr. Herb. 15378*).

The Fawcett specimen is the first record of the species from the province of Jujuy.

7. ERYTHRINA VERNA Vell.

BRAZIL: Maranhão: *Froes 11909.* Bahia: *Froes 12664.*

This is the first record of the species from the States of Maranhão and Bahia.

9. ERYTHRINA SPECIOSA Andr.

BRAZIL: Rio de Janeiro: *Tatto 23* (US).

12. ERYTHRINA EDULIS Triana.

COLOMBIA: Antioquia: *Robledo s.n.* (*Kr. Herb. 15158*). Caldas: *Ramos Nunez s.n.* (*Kr. Herb. 15190*). PERU: Cajamarca: *Stork & Horton 10150* (F). Huanuco: *Stork & Horton 9851* (F). Apurimac: *Stork & Horton 10705* (F).

Local names: Poroton (Ecuador); Pajurro (Peru).

This is the first record of the species from the Department of Cajamarca.

13. ERYTHRINA BREVIFLORA DC.

MEXICO: Michoacan: *Martinez s.n.* (*Kr. Herb. 15346*); *Leavenworth 1914* (M). Morelos: *Martinez s.n.* (*Kr. Herb. 15379*).

14. ERYTHRINA LEPTORHIZA DC.

MEXICO: Mexico: *Hinton 15402.*

16. ERYTHRINA MONTANA Rose & Standl.

MEXICO: Sinaloa: *Gentry 6259* (GH, NY).
This is the first record of the species from the State of Sinaloa.

18. ERYTHRINA PALLIDA Britton & Rose.

TRINIDAD: *Bot. Gard. Trin. 2831* (Trin), *10557* (Trin), *10896* (Trin), *11186* (Trin), *13324* (Trin), *13330* (Trin), *13332* (Trin); *Britton 2656* (type coll., Trin); *Britton & Hazen 230* (Trin); *Dean s.n.* (*Kr. Herb. 15183*).

19. ERYTHRINA MITIS Jacq.

VENEZUELA: Carabobo: *L. Williams 12471* (US).

23. ERYTHRINA AMAZONICA Krukoff.

COLOMBIA: Putumayo: *Cuatrecasas 10647* (US), *11212* (US).
This is the first record of the species from Colombia.

25a. ERYTHRINA CORALLODENDRUM var. BICOLOR Krukoff.

ST. LUCIA: *Ward s.n.* (*Kr. Herb. 15202*).

26. ERYTHRINA CUBENSIS C. Wright.

CUBA: Pinar del Rio: *Acuña s.n.* (*Kr. Herb. 15361*).

27. ERYTHRINA HERBACEA L.

U. S.: Texas: *Parks s.n.* (*Kr. Herb. 15257*), *s.n.* (*Kr. Herb. 15258*), *s.n.* (*Kr. Herb. 15299*), *s.n.* (*Kr. Herb. 15578*). Florida: *Wilmot s.n.* (*Kr. Herb. 15790*); *Killip 32874* (A). MEXICO: Tamaulipas: *Cottam 10564* (*Herb. Univ. Utah*). Oaxaca: *Mexia 9302* (F, M).

28. ERYTHRINA CORALLOIDES DC.

MEXICO: San Luiz Potosi: *Edwards 682* (M). Hidalgo: *Cottam 10491* (*Herb. Univ. Utah*).

29. ERYTHRINA FLABELLIFORMIS Kearney.

MEXICO: Sonora: *Wiggins 7354* (A); *S. White 3126* (GH).

30. ERYTHRINA LANATA Rose.

MEXICO: Michoacan: *Leavenworth & Hoogstraal 1399* (M).

32. ERYTHRINA BERTEROANA Urban.

GUATEMALA: Quezaltenango: *Steyermark 33665* (F). Retalhuleu: *Standley 87847* (F), *87872* (F), *87883* (F), *88413* (F), *88562* (F), *88704* (F). Suchitepequez: *Rosengarten s.n.* (*Kr. Herb. 15141*). Chiquimula: *Steyermark 30932* (F). Santa Rosa: *Standley 78328* (F). Jutiapa: *Standley 75731* (F), *75799* (F); *Steyermark 30382* (F.) COSTA RICA: Guanacaste: *Jorge Leon 961* (CR); *Brenes 12621* (CR), *15507* (CR). Puntarenas: *Brenes 22801* (CR). Alajuela: *Brenes 15042* (CR), *17002* (CR); *Krukoff 3a.* San

Jose: *Skutch 4024* (M). Panama: Panama: *Allen 1631* (F). Chiriqui: *Davidson 735* (A).

This is apparently the first record of this common and widespread species from the Departments of Suchitepequez, Chiquimula and Jutiapa.

32a. Erythrina guatemalensis Krukoff.

Guatemala: Suchitepequez: *Rosengarten s.n.* (*Kr. Herb. 15124*).

The species has been hitherto known only from Baja and Alta Verapaz.

33. Erythrina americana Mill.

U. S.: Alabama: cultivated: *? Parks s.n.* (*Kr. Herb. 15298*). Texas: cultivated: *? Parks s.n.* (*Kr. Herb. 15300*), *? s.n.* (*Kr. Herb. 15301*), *? s.n.* (*Kr. Herb. 15302*). Mexico: Morelos: *Krukoff 1a*. Oaxaca: *Martinez-Calderon 51*.

34. Erythrina Standleyana Krukoff.

Cuba: Pinar del Rio: *Acuña s.n.* (*Kr. Herb. 15403*).

37. Erythrina rubrinervia H. B. K.

Colombia: Caldas: *Ramos Nunez s.n.* (*Kr. Herb. 15193*). Cundinamarca: *Quintero s.n.* (*Kr. Herb. 15234*).

Local names: Chocho colorado (Colombia).

38. Erythrina mexicana Krukoff.

Mexico: Oaxaca: *Mexia 9234* (F). Guatemala: San Marcos: *Giesemann s.n.* (*Kr. Herb. 15129*), *s.n.* (*Kr. Herb. 15365*). Quezaltenango: *Steyermark 33556* (F), *33722* (F). Nicaragua: Granada: *Grant 870*.

This is the first record of the species from Nicaragua. The Guatemalan specimens were collected at altitudes of 1300–1500 meters. Dr. Steyermark states on the labels of his specimens: "Leaves silvery beneath, olive green above, corolla bright red, calyx dull red."

39. Erythrina lanceolata Standl.

Costa Rica: Alajuela: *Brenes 5892* (CR), *11576* (CR), *13200* (CR), *13201* (CR), *13461* (CR), *15006* (CR), *18938* (CR), *21842* (CR), *21989* (CR). Cartago: *Lankester s.n.* (*Kr. Herb. 15377*).

41. Erythrina gibbosa Cufod.

Costa Rica: Alajuela: *Krukoff 2a*; *Brenes 4034* (CR), *4113* (CR), *4866* (CR), *5755* (CR), *9364* (CR), *13202* (CR), *20625* (F). Cartago: *Krukoff 5a*. Panama: Bocas del Toro: *Woodson et al. 1930* (A); *von Wedel 578* (M), *1196* (M). Chiriqui: *Woodson et al. 913* (A). Cocle: *Allen 110* (A).

Local names: Poro de montana (Costa Rica).

On my recent trip to Costa Rica I became acquainted with the species in the field. It is a very spiny small tree, usually 20–25 ft. high and is common along streams on elevations above 1000 meters, at least in the region of Turrialba (Cartago) and in the region of Buena Vista (Alajuela). At the time of my visit to Costa Rica (August) the majority of trees were in flower and a few had immature fruits. Seeds are uniformly scarlet. The species has been hitherto known in Costa Rica only from the provinces of Alajuela, San Jose and Limon.

42. ERYTHRINA PANAMENSIS Standl.

PANAMA: Bocas del Toro: *von Wedel 1766* (M). Canal Zone: *Marjorie Brown 16* (F). Darien: *Terry 1413* (A, F, M).

43. ERYTHRINA COSTARICENSIS M. Micheli.

COSTA RICA: Guanacaste: *Brenes 15636* (CR). Alajuela: *Krukoff 4a.* Cartago: *Jorge Leon 558* (CR), *768* (CR); *Krukoff 6a, 7a, 8a.*

This large forest tree, often up to 80 ft. high, is common along streams on elevations below 1000 meters at least in the region of Buena Vista (Alajuela).

45. ERYTHRINA MACROPHYLLA DC.

GUATEMALA: Quezaltenango: *Standley 87066* (F).

Standley notes on the label: "Rocky open hillside; alt. 1200–1400 meters; small tree, common; flowers bright red."

50. ERYTHRINA VELUTINA Willd.

TRINIDAD: cultivated: *Bot. Gard. Trin. 10042* (Trin). VENEZUELA: Carabobo: *L. Williams 12332* (in part, F).

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THE NORTH AMERICAN VARIATIONS OF DISTICHLIS SPICATA

ALAN A. BEETLE

The genus *Distichlis* of the Gramineae (tribe Festuceae) presents an unusual problem among the grass genera of North America because of its dioeciousness. The members are primarily grasses of alkaline situations, hence the common name "salt grass." This author recognizes three species in North America, *Distichlis spicata* (L.) Greene (a complex consisting of several well marked geographical varieties), *D. texana* (Vasey) Scribn., and *D. palmeri* (Vasey) Fassett. These last two are so easily distinguished by their large size and long spikelets as to need no further discussion here. Outside of North America the genus is represented by *D. distichophylla* (Labill.) Fassett in the south Australian area, in South America by *Distichlis spicata* where again it seems to be broken up into well-defined geographical varieties, and by *D. scoparia* (Kunth) Arech.

Rafinesque (1819) first proposed *Distichlis*, separating it from *Uniola* and *Festuca* and including *D. maritima* (*D. spicata*) and *D. nodosa* (also *D. spicata*). For nearly a century most botanists were content to call all the North American material of this complex one species, whether found on the Atlantic coast, on the Pacific coast, or inland in the dry basins of the West. That the species *Uniola stricta* of Torrey (1824) was but a variety of *D. spicata* was reasoned many times over a long period by Gray (1871 as *Brizopyrum*), Thurber (1880), and Scribner (1894). Recently there has been a tendency to find specific differences between *D. stricta* and *D. spicata;* see Rydberg (1909), Fassett (1925) and Hitchcock (1935). Most of these studies were carried on with reference to a limited amount of California material. It was the additional evidence from this polymorphic group which made the present study seem worth while.

Fassett (1925) has built up the best case for the maintenance of *Distichlis stricta* (Torr.) Rydb. as a species. In his treatment he confines *D. spicata* to the east coast of North America and the Puget Sound region while the rest of the North American material, whether inland or on the California coast, is called *D. stricta*. His separation is as follows:

D. spicata	*D. stricta*
compact panicles	more open panicles
10–20 spikelets	16–24 spikelets
♀ spikelets slightly firmer than the staminate	♀ spikelets firm and coriaceous, the staminate papery
spikelets 4–9-, rarely 12-flowered	spikelets 6- to 18-flowered
lemmas 4.5–7.8 mm. long (except in a few plants)	lemmas 3.2–5 mm. in length

D. spicata	*D. stricta*
grain 2 mm. long, ovoid, and not much narrowed below the two beak-like styles	grain 2.5–5 mm. long, narrowed to an attenuate style, which is sometimes split, but hardly into two distinct styles
leaves smooth-edged and blunt or oblique at the tip	leaves sharp-pointed and serrate at the tip

That *Distichlis dentata* Rydb., "described as differing from *D. spicata* and *D. stricta* in having broader leaves, spikelets, glumes and paleas and dentate keels on the paleas," differs "only in degree" was concluded by Fassett, and has recently been corroborated by Reeder (1943). This conclusion is again reached here but it is further maintained that the differences between *D. spicata* and *D. stricta* are not sufficiently constant to treat the entities as more than geographical varieties.

There are no more compact spikes (either staminate of pistillate) than those found in the material from coastal California; on this character as well as leaf serration and tip, and achene measurement the material should fall with *D. spicata*, but, as pointed out by Fassett (1925), the characters of the palea and lemma are closer to those of *D. stricta*. The number of spikelets in material from California has been found to vary from 3 to 60 in pistillate plants and from 3 to 20 in staminate plants. The great variation in texture of both the palea and the lemma, usually correlated with the width of the base of the lemma, is recognized, but no pattern of discontinuity has been discovered. In general the plants which Hitchcock has maintained represent *D. stricta* as opposed to *D. dentata* have narrow spikelets with less firm lemmas and paleas and lack the conspicuously dentate palea wings. There is certainly no dividing line. Some specimens from California are no different in texture from those of the Atlantic coast. The number of florets in a spikelet in California material has been counted from 3 to 14 in pistillate plants and from 3 to 20 in staminate plants. The variation in both shape and size measurements of the grains is very confusing. Some of the seeds have a slender attenuate tip while others have an abruptly truncate tip, and every length between 1.5 and 3.5 mm. has been found in apparently fully mature material from western North America. As a result of the foregoing it is concluded that *D. stricta* is not specifically distinct from *D. spicata*.

In reaching this decision it is not sufficient to study only the North American material. There are thirteen independent names (*D. ammobia, araucana, hirta, humilis, laxiflora, marginata, mendocina, misera, prostrata, tenuifolia, thalassica, viridis, volckmanni*) for South American material, which, in light of the heavy conspecificity between the two continents, have a definite bearing on the problem. That other botanists who have dealt with this South American material consider *D. spicata* a single polymorphic species composed of many geographical varieties is indicated by the combinations *D. spicata* var. *humilis* (Phil.) O. Kuntze, var. *marginata* (Phil.) O.

Kuntze., var. *thalassica* (H. B. K.) Ktze., and *D. spicata* var. *mendocina* Hack. Although these varieties are considered to belong to the same species as the North American varieties, they have marked differences, e.g., culm pubescence, and as yet it has not been determined with certainty that any of the varieties occur on both sides of the equator.

Actually it is not enough merely to decide taxonomically that all the strains of a complex comprise a given species. Often names for the entities in subspecific categories are very important. *Distichlis* is one of the few perennial grasses of prostrate habit, spreading by rhizomes (or rarely by stolons) which is adapted to alkaline soils. In the west where large areas are alkaline, covers for air fields and playgrounds are important but difficult to establish. Although *Distichlis* will probably never be highly recommended for forage it seems that some of the strains are much more palatable if not more nutritious than others. An analysis of the various California types seems therefore well justified from a utilitarian standpoint.

Observations in the field tend to indicate that male and female plants occur with approximate frequency throughout the whole range, although often only one or the other is present in a limited area because of vegetative propagation. Although pollen is freely produced and pistillate plants flower abundantly, mature seed is seldom set probably because of (a) the separation into male and female colonies, (b) the extreme xerophytic nature of the habitat which often does not allow sufficient time for full development. Of 332 North American collections of the *Distichlis spicata* complex available for study, which may be taken to comprise a random sampling, 143 were pistillate only, 22 had both pistillate and staminate plants, and 167 were staminate only. As noted by Reeder (1943) there is a noticeable predominance of staminate plants in the *D. stricta* group. Where plants are only vegetative no way has been discovered to determine whether they are male or female, but it is usually possible to determine to what variety they belong on vegetative characters. Even the staminate and pistillate spikes, as mentioned by Hitchcock (1935), are very similar, usually differing to a marked degree only in the palea.

Stebbins and Love (1941) reported $2n = 40$ for *Distichlis*, the only chromosome number reported for California material. Holm (1891) was able to recognize as distinct North American entities, based on anatomical evidence, the following: *D. maritima* (Atlantic coast), *D. maritima* var. *stricta* (Nebraska), *D. maritima* var. *laxa* (Utah), *D. thalassica* H. & K. (Lower California), *D. prostrata* (Mexico). This author is unable to appraise the significance of the rather incomplete data.

California material of *Distichlis* often displays insect galls caused by the fly, *Chlorops graminea* Coq.

Since much of the confusion in determining plants in the past has been over staminate and pistillate plants it was decided here to treat each separately. The plants were first separated arbitrarily into males and females and then separated into units on the basis of the female plants only. It was then considered significant that the male plants from the same region had the same vegetative characters.

In the preparation of this paper material from the following herbaria has been examined: Agronomy Division Grass Herbarium (AG), College of Agriculture, Univ. of California, Davis; Botany Department, University of California (UC), Berkeley; Dudley Herbarium (D), Stanford University; California Academy of Sciences. In the interest of brevity the source of the specimens except types will not be further specified.

DISTICHLIS RAFINESQUE

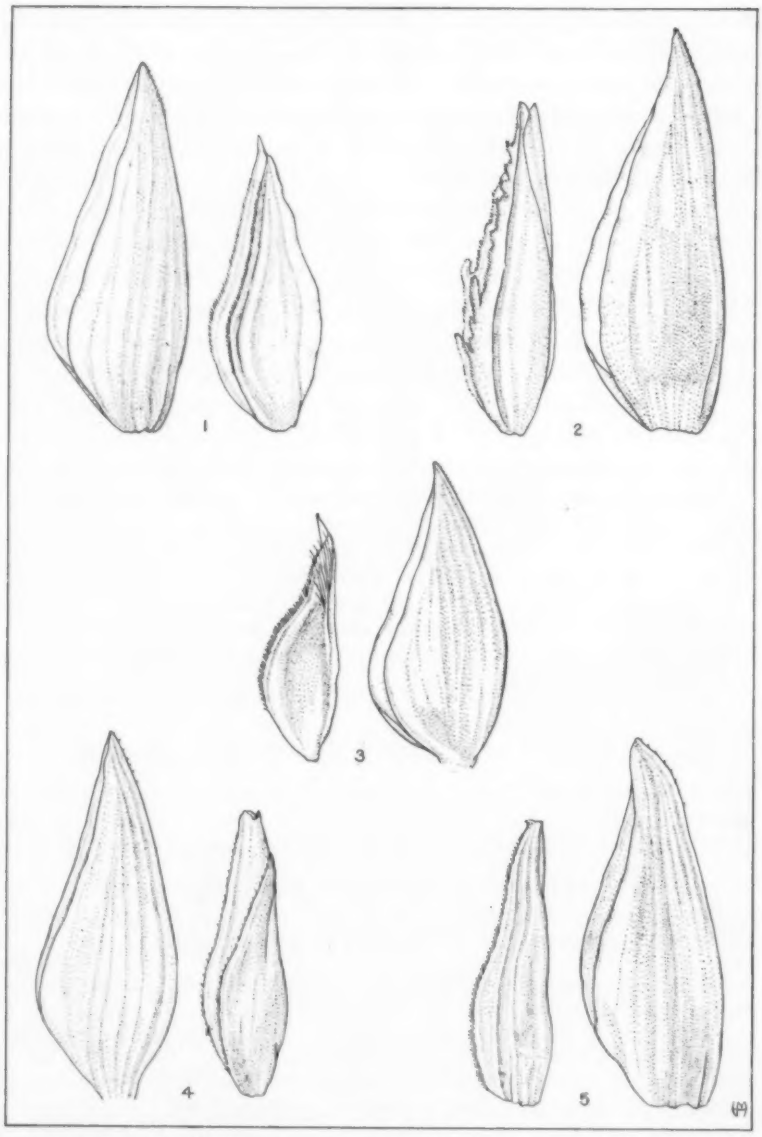
Dioecious perennials; culms wiry, upright from strong, creeping, or deeply-running rhizomes; ligule short and evenly serrate; leaf-blades noticeably, often stiffly 2-ranked, flat or somewhat involute; staminate spike exceeding the blades, the blades usually equalling or exceeding the pistillate; spikelets in open or dense spikes, few to many flowered; glumes unequal, broad, 3–7 nerved; lemmas closely to loosely inbricate, 9–11 nerved, coriaceous; palea usually a little shorter than the lemma, two keeled, serrate on the keels, often with a few long hairs on the back, the nerves sometimes excurrent; caryopsis brown; stamens 3.

Plants pistillate

- Spikes congested, the short pedicels hidden, of uniformly 5–9 flowered spikelets
  - Spikes narrow, culms strictly erect, never stoloniferous, often 3–6 dm. long
    - Outer glume 3 mm. long, second glume 4 mm. long; lemma ca. 6–10 nerved ..... 1. *D. spicata*
    - Outer glume 2.5 mm. long, second glume 3 mm. long; lemma ca. 12–14 nerved ..... 2. *D. spicata* var. *borealis*
  - Spikes oval, culms usually prostrate, often stoloniferous, up to 3 dm. long ..... 3. *D. spicata* var. *stolonifera*
- Spikes of approximate but rarely congested spikelets, the pedicels readily visible, the number of florets very variable (3–14)
  - Leaves divaricate, culms and leaves rigid ..... 4. *D. spicata* var. *divaricata*
  - Leaves mostly ascending, culms and leaves lax
    - Blades long (1–2 dm.), equally spaced on the culm, often equalling or exceeding the spikes; spikelets 4–6 mm. broad ..... 5. *D. spicata* var *stricta*
    - Blades short, seldom 1 dm. long, usually crowded at the base, and exceeded by the spikes, spikelets 2–4 mm. broad
      - Palea broadly winged at base, usually hairy on the back ..... 6. *D. spicata* var. *nana*
      - Palea narrowly winged at base, glabrous on the back ..... 7. *D. spicata* var. *mexicana*

Plants staminate (a rudimentary pistil often present)

- Spikes congested, of uniformly 5–9-flowered spikelets, the blades usually equalling the spike



FIGS. 1–5. Sample pistillate lemmas and paleas of the *Distichlis spicata* complex. FIG. 1. *D. spicata* var. *borealis*, drawn from Vancouver Island material. FIG. 2. *D. spicata* var. *stricta*, drawn from *Sandberg & Leiberg 468*, the co-type of *D. dentata*. FIG. 3. *D. spicata* var. *nana*, drawn from the type. FIG. 4. *D. spicata* var. *stolonifera*, drawn from the type. FIG. 5. *D. spicata* var. *mexicana*, drawn from the type.

Culms strictly erect, spikelets pale green or slightly purplish
Florets mostly 5–6 per spikelet; leaves 1–2.5 cm. apart on culm usually ..... 1. *D. spicata*
Florets mostly 7–10 per spikelet; leaves 1.5–6 cm. apart on culm ..... 2. *D. spicata* var. *borealis*
Culms somewhat prostrate, often stoloniferous; spikelets strongly purplish ..... 3. *D. spicata* var. *stolonifera*
Spikes approximate but rarely congested; the blades not usually equalling the spike
Leaves divaricate, culms and leaves rigid ..... 4. *D. spicata* var. *divaricata*
Leaves mostly ascending, culms and leaves lax
Blades long (1–2 dm.); spikelets 4–6 mm. broad ..... 5. *D. spicata.* var. *stricta*
Blades short, seldom up to 1 dm. long; spikelets 3–4 mm. broad
First glume 2 mm. long, second glume 3 mm. long; anthers 2 mm. long ..... 6. *D. spicata* var. *nana*
First glume 3 mm. long, second glume 4 mm. long; anthers 3 mm. long ..... 7. *D. spicata* var. *mexicana*

1. DISTICHLIS SPICATA (L.) Greene.

Culms 1–6 dm. tall, slender, erect; blades erect up to 1.5 dm. long, 1–2.5 cm. apart on the culm; equaling or exceeding the pistillate spikes and rarely exceeded by the staminate spikes; pistillate spikes pale green, 1–6 cm. long, of 8–36 congested spikelets, these spikelets 5–9 flowered, up to but not exceeding 1 cm. long, 4 mm. broad, the first glume 3 mm., second glume 4 mm. long, the lemmas 6–10 nerved, 3.5–4 mm. long, closely imbricate, the palea 2-keeled, the keels minutely, evenly serrate, the 4 nerves often excurrent; caryopsis ca. 2 mm. long, somewhat truncate at the tip.

Staminate spike pale green, 1–6 cm. long, of 6–30 congested spikelets; the spikelets 7–10 flowered, ca. 1 cm. long, 4 mm. broad, the first glume up to 3 mm. long, the second glume up to 4 mm. long, the lemmas 6–10 nerved, 3 mm. long, the palea 2 keeled but otherwise nerveless, ca. 3 mm. long; anthers ca. 2–3 mm. long.

Type locality: Atlantic Coast of North America.

Range: Coastal salt marshes, Prince Edward Island to Florida; West Indies; Louisiana; Texas.

Since any of the collections made in this range may be considered representative of typical *Distichlis spicata* (L.) Greene, no specimens will be cited.

2. D. SPICATA var. **borealis** (Presl) Beetle, comb. nov.

Brizopyrum boreale Presl, Rel. Haenk. **1**: 280. 1830.

Culms 2–4 dm. tall, erect; blades erect, exceeding the pistillate spikes and rarely exceeded by the staminate; pistillate spikes pale green or slightly purplish, 2–6 cm. long, of 10–60 congested spikelets; the spikelets ca. 1 cm. long, 4 mm. broad, 5–9 flowered, the florets closely imbricate, the first glume 2.5 mm. long, second glume 3 mm. long, the lemmas 12–14 nerved, 4.5 mm. long; the palea 3.5 mm. long, evenly serrate on the keels, nerveless, the caryopsis ca. 2 mm. long, somewhat truncate at the tip. (Figs. 1, 8.)

Staminate spikes pale green or slightly purplish, 2.5–5 cm. long, of 6–30 congested spikelets, the spikelets up to ca. 1 cm. long, 4 mm. broad, 5–0 flowered, the florets closely imbricate, the first glume ca. 3 mm. long, second glume 3.5 mm. long, the lemmas 4.5 mm. long, 8–12 nerved, usually not

scabrous on the back, the palea 3.5–4 mm. long, serrate on the keels, nerveless; anthers ca. 3 mm. long.

Type locality: Nootka Sound, Vancouver Island, *Haenke*.

Female: British Columbia, Crescent Beach, *Eastham 9920*, Cadboro Bay, *Pineo* in 1894. Washington, Clallam Co., *Elmer 1667*; San Juan Co., *Roush* in 1919; Twin Island, *Berg 32*, King Co., *Thompson 5232*. Male: British Columbia, Sooke Harbor, *Pineo* in 1898. Washington, Whatcom Co., Kitsap Co., *Otis 1635*.

Distichlis spicata var. *borealis* is in many respects intermediate between the typical material on the east coast of North America and *D. spicata* var. *stolonifera*. The Puget Sound material has the tall erect habit of typical *D. spicata* as well as the narrow spikes but in the purplish color of the spikes and many of the technical measurements suggests the var. *stolonifera*.

3. D. SPICATA var. **stolonifera** Beetle, var. nov.

Culms up to 3 dm. tall, often prostrate, with a strong tendency to produce stolons; blades erect, mostly 1–2 dm. long, the upper exceeding the pistillate spike and usually equalling the staminate; pistillate spike green or often strongly purplish, oval, club-shaped, 1.5–5 cm. long, often 2 cm. thick, of 8–35 congested spikelets, the spikelets 5–9 flowered, closely imbricate, ca. 1 cm. long or rarely longer, 4 mm. broad, the outer glumes 2.5 mm. long, second glume 3.5 mm. long, the lemmas 5 mm. long, faintly nerved, the palea 2-keeled, broadly winged below, with very hyaline margins, serrate on the keels above but smooth at the base, caryopsis ca. 2 mm. long, broadest at the base, slightly truncate at the tip. (Figs. 4, 12.)

Staminate spikes green or often strongly purplish, 1.5–5.5 cm. long, of 6–20 congested spikelets often interrupted below, the spikelets 7–10 flowered, ca. 1 cm. long, 4 mm. broad, the first glume ca. 3 mm. long, the second glume ca. 3.5 mm. long, the lemmas 3.5 mm. long, faintly nerved and weakly scabrous, the palea subequal with or slightly longer than the lemma, the keels minutely, evenly serrate above, the margins hyaline, nerveless, anthers 2.5 mm. long. (Fig. 7.)

Culmi saepe prostratae, saepe stoloniferae; spicae feminae viride aut saepe forte purpurascentes, ovatae, cum 8–35 congestae spiculae; spiculae cum 5–9 florae. Spicae masculinae viridae aut saepe forte purpurascentes, cum 6–20 congestae spiculae; lemmae circa 3.5 mm. longae; paleae subaequalae, bicarinatae.

Type locality: near Ferndale, Humboldt Co., California (pistillate), July 30, 1899. *J. B. Davy & W. C. Blasdale 6202* (UC). Co-type: Arcata, Humboldt Co., California (staminate), June 17, 1899. *J. B. Davy & W. C. Blasdale 5604* (UC).

Female: California, Humboldt Co., Eureka, *Yates 5859*; Marin Co., Point Reyes, *Davy 6736*; Contra Costa Co., Point Richmond, *Beetle 1752*; Alameda Co., West Berkeley, *Davy 856*; near San Francisco, *Bolander 1527*; San Mateo Co., *Beetle 1888*; Santa Cruz Co., Santa Cruz, *Thompson* in 1903; Monterey Co., Monterey, *Elmer 4042*; Orange Co., s. of Laguna Beach, *Beetle 3099*; San Diego Co., Coronado, *Chandler 5164*.

Male: Oregon, Netarts, *Thompson 3150*. California, California, Humboldt Co., Eureka, *Stebbins & Church 3104*; Mendocino Co., Fort Bragg, *Davy & Blasdale 6125*; Marin Co., *Davy 4039*; Contra Costa Co., *Wiesendanger 1534*; Alameda Co., Hayward, *Nixon* in *1915*; San Francisco, *Bolander 1527*; Santa Clara Co., near Alviso, *Dudley* in 1903; Monterey Co., Del Monte, *Elmer 4042*; Santa Barbara Co., Santa Barbara, *Elmer*

3902; Los Angeles Co., Pebble Beach, *Fosberg 84475;* Orange Co., s. of Laguna Beach, *Beetle 3099.*

The most characteristic and strongly stoloniferous material of this variety is found at certain points along the coast, namely at Humboldt Bay, San Francisco Bay, Monterey Bay and Orange County. Material from other points along the coast is less stoloniferous but agrees in technical points. In the coast hills and inland marshes there is a considerable amount of intergradation, although most of this material is nearer to var. *stricta.*

4. D. SPICATA var. **stricta** (Gray) Beetle, comb. nov.

Brizopyrum spicatum var. *strictum* A. Gray; S. Wats., in King, Geol. Expl. 40th Par. 5: 385. 1871. (Based on *Uniola stricta* Torr.)

Culms 1–3.5 dm. tall, erect or rarely decumbent, the blades up to 2 dm. long, the upper equalling or exceeding the pistillate spikes but exceeded by the staminate; pistillate spike green drying straw brown, 2–7 cm. long; of 5–40 approximate spikelets, the spikelets 0.5–2 cm. long, 5–20-flowered, 4–7 mm. broad, the mature florets often strongly reflexed, usually not closely imbricate, the first glume 2–3 mm. long, the second 3–4 mm. long, the lemma 3.5–6 mm. long, firm, with a broad hyaline margin, the palea 3–5 mm. long, the keels conspicuously serrate to the base, often dentate, narrow or winged at the base, occasionally with a few long hairs on the back, the caryopsis 2–5 mm. long, sometimes slenderly tapered to a single beak, sometimes truncate with a double beak. (Figs. 2, 11, 13.)

Staminate spike green or rarely purplish, drying straw brown, 2–5 cm. long, of 5–25 approximate spikelets, the spikelets 0.5–2 cm. long, 5–20-flowered, 4–7 mm. broad, closely imbricate, the first glume 2–3 mm. long, the second 3–4 mm. long, the lemmas 5–6 mm. long, firm, equaled by the palea, the palea 5–6 mm. long, the keels conspicuously serrate to the base, infrequently dentate, rarely broadly winged, usually with at least one prominent marginal vein, the anthers 3–4 mm. long. (Fig. 6.)

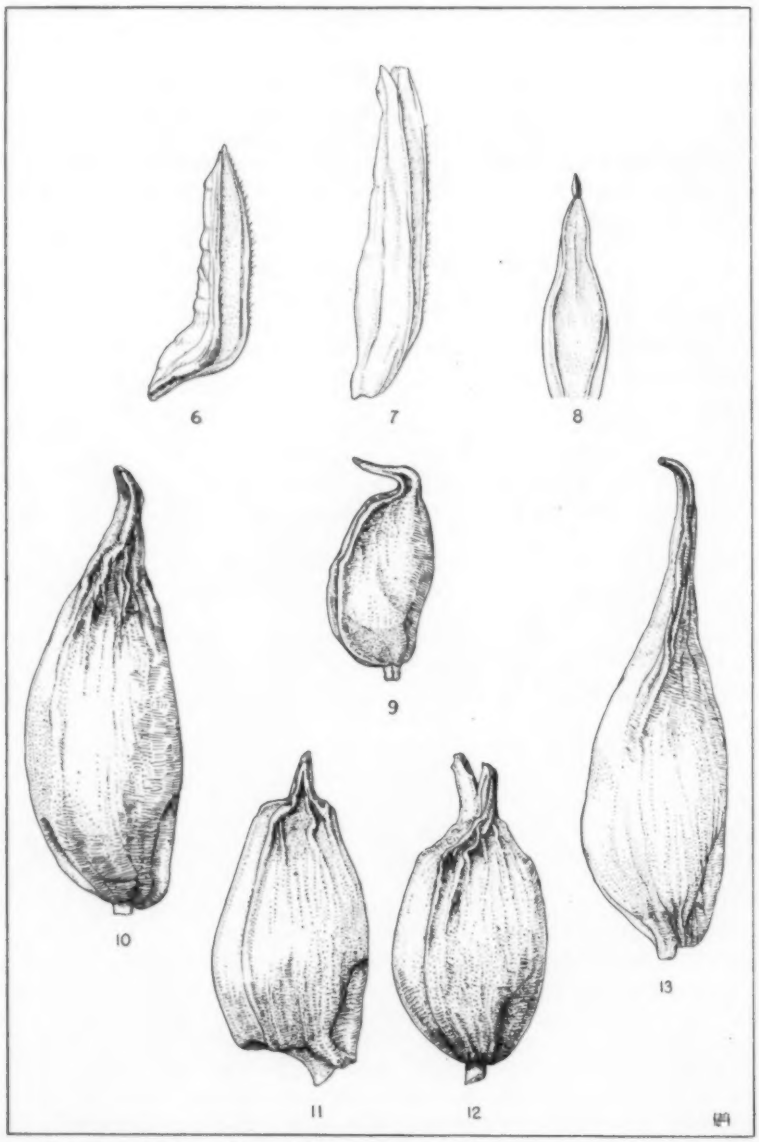
Type locality: Canadian River, Oklahoma.

Range: Alkaline situations; Saskatchewan south through N. D., S. D., Kansas, Nebraska, Oklahoma, and Texas and west to the Pacific Coast.

D. spicata var. *stricta* has the widest range of any of the varieties. In various parts of its range it approaches in certain characters all the other varieties and even the typical material from the eastern seaboard. The amazing variations in the caryopsis suggests the following hypothesis. *Distichlis* might be called an evergreen grass. It needs only sufficient warmth and moisture to start new growth. Yet its xerophytic habitat seldom gives it a prolonged period of growth for most of the time it is either too cold or too dry. Some achenes are produced in the cold wet winters and some in the hot, dry summers and many are caught in a partially mature condition when growth ceases. It is very possible that here is a case in which some of the reproductive structures are of less importance than the vegetative.

In California the range of the species is disrupted by the Sierra Nevada and Tehachapi Mountains.

Modoc County, *Manning 423,* Siskiyou Co., *Butler 1844;* Lassen Co., *Beetle 2807;* Glenn Co., *Davy* in 1898; Sierra Co., *Lemmon* in 1874; Colusa Co., *Beetle 3270;* Yolo Co., *Raynor* in 1939; Alameda Co., *Yates 5503;* Mono Co., *Rose 35416;* Merced Co.,



FIGS. 6–8. Staminate paleas. FIG. 6. *D. spicata* var. *stricta*, drawn from Santa Barbara Co., Calif., material. FIG. 7. *D. spicata* var. *stolonifera*, drawn from Alameda Co., Calif., material. FIGS. 9–13. Sample grains of the *D. spicata* complex. FIG. 9. *D. spicata* var. *nana*, drawn from Merced Co., Calif., material. FIG. 10. *D. spicata* var. *divaricata*, drawn from Imperial Co., Calif., material. FIG. 11. *D. spicata* var. *stricta*, drawn from *Sandberg & Leiberg 468*, the co-type of *D. dentata*. FIG. 12. *D. spicata* var. *stolonifera*, drawn from San Mateo Co., Calif., material. FIG. 13. *D. spicata* var. *stricta*, drawn from Nebraska material.

Howell 2046; Kings Co., *Beetle 2981;* Tulare Co., *Palmer 2754;* Inyo Co., *Beetle 3669;* Kern Co., *Davy 1842;* San Luis Obispo Co., *Johannsen 1190;* Ventura Co., *Simontacchi 112;* San Bernardino Co., *Beetle 3204;* Orange Co., *Wolf 3785;* Riverside Co., *Koethen* in 1897; San Diego Co., *Chandler 5227.*

5. D. SPICATA (L.) Greene var. **nana** Beetle, var. nov.

Culms erect, very slender, 1–4 dm. tall, the blades up to 6 dm. long, rarely longer, exceeded by both the staminate and pistillate spikes, often crowded at the base, the pistillate spikes green or purplish, drying brown, 1–4 cm. long, of 3–12 approximate spikelets, the spikelets 0.5–2 cm. long, 3–18-flowered, 3–4 mm. broad, closely imbricate, the first glume ca. 3 mm. long, the second glume 3.5 mm. long, the lemmas ca. 3.5 mm. long, very broad at the base, 9-nerved, the palea subequal, very strongly ciliate on the keels, abruptly winged below, with a single prominent marginal nerve, the caryopsis ca. 2 mm. long, abruptly truncate at the apex, the apex often bent. (Figs. 3, 9.)

Staminate spike green or purplish, drying brown, 1–4 cm. long, of 3–12 approximate spikelets, the spikelets 0.5–2 cm. long, 3–16-flowered, 3–4 mm. broad, closely imbricate, the glumes ca. 3 mm. long, the lemma ca. 3.5 mm. long, broad at the base, 9-nerved, the palea subequal, evenly ciliate on the narrow keels, anthers ca. 2 mm. long.

Culmi erectae, summe graciles, 1–4 dm. alti, laminae generalis usque ad 6 dm. longae, saepe basi confluenti, spicae feminae viride aut purpurascentes, cum 3–12 propinquae spiculae; spiculae propinquemente imbricatae, cum 3–18 florae, lemmae circa 3.5 mm. longae; paleae subaequalae, bicarinatae. Spicae masculinae viridae aut purpurascentes, cum 3–12 propinquae spiculae, spiculae cum 3–16 florae.

Type locality: California, Tulare County, Whitaker Forest, June 28, 1928, P. B. Kennedy (AG). Co-type: California, Kern County, near Bakersfield, 1896, *J. B. Davy 1841* (UC).

Female: California, Tehama Co., w. of Red Bluff, *Beetle 3285;* Kern Co., McKittrick, *Yates 6511;* Tulare Co., Whitaker Forest, *Kennedy* in 1928; Santa Barbara Co., w. of Cuyama Ranch, *Beetle 3031;* Merced Co., e. of San Joaquin R., *Stebbins 2798;* Stanislaus Co., w. of Modesto, *Beetle 2944;* Monterey Co., s.w. of Bradley, *Grahm 376;* San Diego Co., Escondido, *Meyer 454;* Lassen Co., Amedee, *Davy* in 1897.

Male: California, Stanislaus Co., *Sharsmith 3777;* Kings Co., s. of Armona, *Beetle 2967;* Kern Co., near Delano, *Davy 2446;* Tulare Co., Visalia, *Dudley* in 1900; Alameda Co., n.w. of Halfway House, *G. L. Stebbins 2736;* Fresno Co., Huron, *Eastwood* in 1893.

This variety is often reported collected on soils which seem to be hardly if at all alkaline. It has the finest leaves and would seem to be the most palatable for stock.

6. D. SPICATA (L.) Greene var. **divaricata** Beetle, var. nov.

Culms 1–4 dm. tall, very stiffly erect, the blades rarely exceeding 5 cm. in length, rigid, divaricate, exceeded by both the staminate and pistillate spikes, the pistillate spike green or purplish quickly turning brown, 2–6 cm. long of 6–20 approximate spikelets, the spikelets 0.5–1.5 cm. long, 5–12-flowered, 3–6 mm. broad, the first glume 3 mm. long, the second glume 3–3.5 mm. long, the lemma ca. 4 mm. long, broad below, without prominent nerves, the palea ca. 3.5 mm. long, often dentate, conspicuously serrate on the keels.

usually without prominent nerves, the caryopsis 2–3 mm. long, plump, usually somewhat tapered to a single apex. (Fig. 10.)

The staminate spike green or purplish quickly turning brown, 2–6 cm. long, of 6–15 approximate spikelets, the spikelets 0.5–1.5 cm. long, 5–12-flowered, 3–6 mm. broad, the first glume ca. 3 mm. long, the second glume nearly subequal, the lemmas ca. 4 mm. long, broad below, without prominent nerves, the palea subequal, very narrow, nerveless, the anthers 2–2.5 mm. long.

Culmi 1–4 dm. alti, summe erecti rigide, laminae generalis usque ad 5 cm. longae, rigidae, divaricatae; spicae feminae viride aut purpurascentes, cum 6–20 propinquae spiculae, spiculae cum 5–12 florae, lemmae sinae prominentae nervae; paleae saepe dentatae; gramen pinquis. Spicae masculinae viridae aut purpurascentes, cum 6–15 propinquae spiculae, spiculae cum 5–12 florae, sine prominentae nervae; paleae subaequalae, summe angustae, sine nervae.

Type locality: California, Riverside Co., Salton, *J. B. Davy* in 1902 (UC). Co-type, California, Imperial Co., Salton Sink, March 17, 1917, *E. A. McGregor 779* (Dudl).

Female: California, Kern Co., near Rosamond, *Davy 2944;* Mexico, western Sonora, 1898, *W. W. Price;* Sonora, *Wiggins 8587,* Baja Calif., *Wiggins & Gillespie 4171.*

Male: California, Mojave, *M. E. Jones* in 1917, Death Valley, *Grinnell* in 1917. Mexico, Baja Calif., n. of Ensenada, *Wiggins & Gillespie 3920.*

7. DISTICHLIS SPICATA (L.) Greene var. **mexicana** Beetle, var. nov.

Culms 1–3 dm. tall, erect, rather slender; blades erect, up to 1 dm. long, the upper about equalling the pistillate spikes and exceeded by the staminate, the pistillate spike green, 3–5 cm. long, of 6–16 approximate spikelets, the spikelets 0.5–1.5 cm. long, 3–4 mm. broad, the upper often curved, of 3–12 florets, the first glume ca. 3 mm. long, the second 3.5 mm. long, the lemma prominently 9-nerved, very broad below with a hyaline margin, ca. 5 mm. long, the palea subequal, serrate on the often dentate keel, with a single prominent marginal vein, the caryopsis plump at the base, gradually tapered to the apex. (Fig. 5.)

Staminate spike green or purplish, 1.5–8 cm. long, of 6–15 approximate spikelets, the spikelets 0.5–1.5 cm. long, 3–4 mm. broad, the upper often curved, of 3–12 florets, the first glume ca. 2 mm. long, the second 3–3.5 mm. long, the lemmas prominently 9-nerved, broad below, with a hyaline margin, the palea subequal, serrate on the keels, narrow above and slightly broadened below, the anthers 3–4 mm. long.

Culmi 1–3 dm. alti, erecti, aliquanti graciles; laminae erectae, usque ad 1 dm. longae; spicae feminae cum 6–16 propinquae spiculae, spiculae superioribus saepe flexi, cum 3–12 florae, lemmae et paleae subaequalae. Spicae masculinae, viridae aut purpurascentes, longae, cum 6–15 propinque spiculae, spiculae superioribus saepe flexi, cum 3–12 florae.

Type locality: Mexico, city of Durango, 1896, *E. Palmer 388* (UC) (pistillate). Co-type: Mexico, city of Durango, *E. Palmer 182* (UC) (staminate).

Mexico, Valley of Mexico, 1897, *C. G. Pringle 6640.*

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INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

The Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of three cents for each card. **The different subjects as classified below may now be ordered separately** (but no orders will be taken for less than one year's issue in any classification). Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

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(exclusive of fungi)

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